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BY

LAMBERT BEVERLY TARLO

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By L. B. TARLO

CONTENTS

SYNOPSIS

A systematic review is made of the thirty-six known Upper Jurassic Pliosaur species and of these only nine, representing five genera, are shown to be valid. These valid species are described and detailed comparisons made between them based on the characters of the teeth, cervical vertebrae, mandibles and scapulae. The remaining species are briefly discussed and listed in alphabetical order of their trivial names. Finally, a fully illustrated key is given for the identification of Pliosaurs.

I. INTRODUCTION

In Mesozoic times several groups of reptiles left the land to take up life again in the sea. Of these marine reptiles the plesiosaurs are perhaps the best known. The first specimens were discovered at the beginning of the last century by Miss Mary Anning who made her living collecting and selling fossils; and the Rev. Dean Conybeare, who gave the earliest description of the plesiosaurs, made the important

observation that there were forms with long necks and others with a much shorter neck (see Text-fig. 1). This review is concerned solely with the latter group which were given the name of pliosaurs after the genus *Pliosaurus* had been created by Owen in 1841.

Most of the short-necked plesiosaurians (or pliosaurs) of which the Upper Jurassic species form the central group, were described during the nineteenth century from England, France, Germany and Russia. Unfortunately there is much confusion in the literature. Some species were erected on isolated humeri and femora, some on

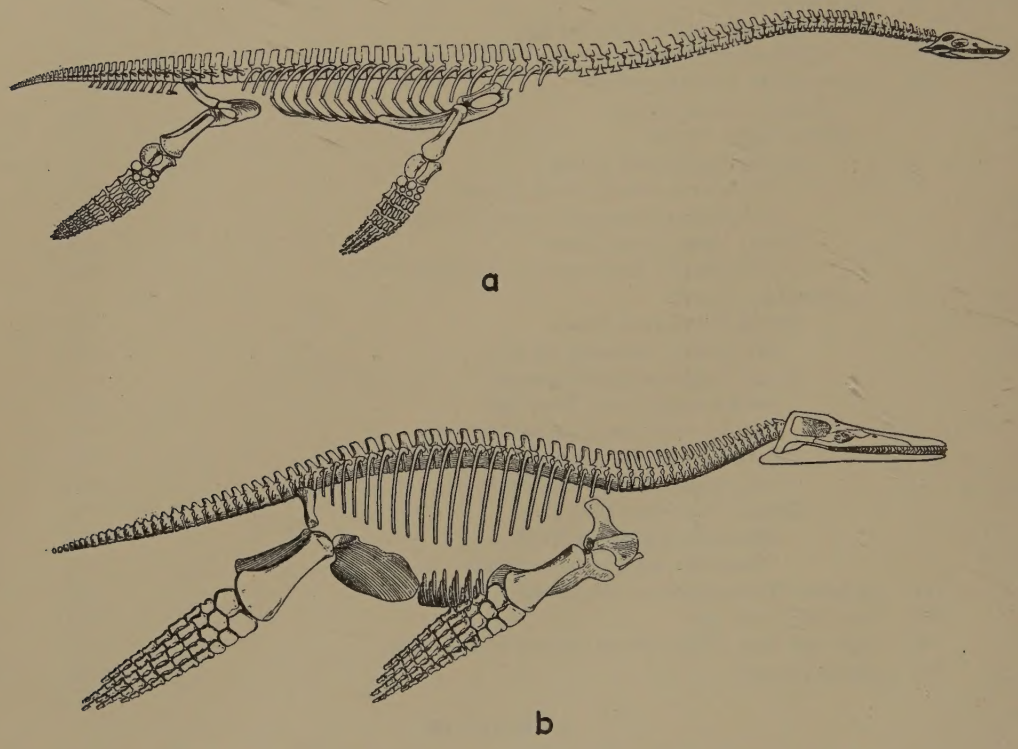

FIG. 1. *a*. Reconstruction of the Liassic *Plesiosaurus dolichodeirus* Conybeare, after Conybeare (1824). *b*. Reconstruction of the Oxfordian *Peloneustes philarchus* (Seeley), after Andrews (1913).

teeth alone and yet others only on vertebrae ; and Seeley (1869) seemed to differentiate some of his species on size. Confusion was added to by authors ignoring the work of fellow palaeontologists—for example, P. Fischer and E. Deslongchamps both gave detailed descriptions and figures of identical specimens under different names. Even more unfortunate, however, was the obvious feud between Seeley and Lydekker, who steadfastly refused to recognize the generic and specific names proposed by one another. *Rhomaleosaurus* Seeley was, according to Lydekker, a synonym of *Thaumatosaurus*, whilst *Peloneustes* Lydekker was always claimed by Seeley to be

Pliosaurus ; in addition, Seeley's specific names were generally stated by Lydekker to be synonyms of names erected years later, such as *P. sterrodeirus* Seeley (1869) taken as a synonym of *P. aequalis* Phillips, 1871. Worse still were the discrepancies in the straightforward descriptions of actual specimens. One notable mandible stated by Owen (1869) to have 24 teeth in each ramus, was later recorded by Lydekker (1889*b*) as having 30. There are in fact 25 in one ramus and 26 in the other.

Although an abundance of isolated pliosaur fragments has been described, I have concentrated attention on associated specimens, and in this way have been better able to compare the different species. The parts of the skeleton which I have found useful in making comparisons among the different species are : teeth, mandibles, cervical vertebrae, scapulae and epipodials (radii, ulnae, tibiae and fibulae). Some parts, such as the propodials (humeri and femora) are of very limited value and appear to be indistinguishable from one species to another. The teeth appear to be more useful, serving primarily to separate the Kimeridgian pliosaurs, in which the teeth are trihedral in cross-section, from those of Oxfordian age, in which they are circular. All pliosaur teeth are characterized by longitudinal ridges on the enamel of the crown, and in the Kimeridgian all the teeth of the three known species have the same ornamentation. In the Oxfordian, however, the patterns of these ridges vary and can be used to separate the six species from one another.

On the whole specific distinctions can best be effected on the characters of the cervical vertebrae, in particular the presence or absence of a ventral keel. Even this, however, must be used with caution as in all forms where a ventral keel is present it disappears towards the back of the neck where the rib articulation begins to rise from the centrum on to the neural arch.

The differences in the mandibles and scapulae are of more fundamental biological significance, and can be used as the basis for generic distinctions. Mandibles fall into two main groups both of which persist through Oxfordian and Kimeridgian times. One group, typified by *Liopleurodon ferox*, has a short symphysis which bears 5–7 pairs of large caniniform teeth, whilst the other, typified by *Pliosaurus brachydeirus*, has a longer symphysis with about 6 pairs of large caniniform teeth but with the addition of a further 5–6 pairs of smaller teeth. In Oxfordian times there were two extreme forms—*Simolestes* with a short spatulate symphysis, and *Peloneustes* with a greatly elongated symphysis.

All Oxfordian scapulae are triradiate with the dorsal process produced laterally and set off at an angle to the plane of the bone, from a ridge running from the glenoid ramus to the anterior point of the ventral plate. During the Kimeridgian striking changes took place in this bone. *Stretosaurus* has a scapula all in one plane in which the dorsal process is produced anteriorly, thus increasing the pre-glenoid length of the whole pectoral girdle. It has recently been established (Tarlo, 1959*a*) that the type of scapula common to all Oxfordian species is restricted in Kimeridgian times to pliosaurs with a long mandibular symphysis, while the *Stretosaurus* type of scapula belongs to those with a short symphysis.

This study has shown that the different skeletal elements fall into two groups—those which change with geological age and affect the whole group, such as teeth and epipodials, and those which persist through time and indicate possible phylo-

genetic relationships, as exemplified by mandibles. As already mentioned, the teeth and epipodials can generally be used to distinguish Oxfordian from Kimeridgian pliosaurs, while the different forms of mandible found in both ages indicate two separate lineages which can be recognized in Kimeridgian times on their radically different scapulae.

A brief description of the nine Upper Jurassic pliosaur species, which are all I now consider valid out of an original thirty-six species, is given below, and their possible phylogenetic relationship to one another is shown in Text-fig. 2. The remaining species are considered in further sections, and at the end of this paper I have given a key to the valid species which it is hoped will facilitate the identification of isolated skeletal elements.

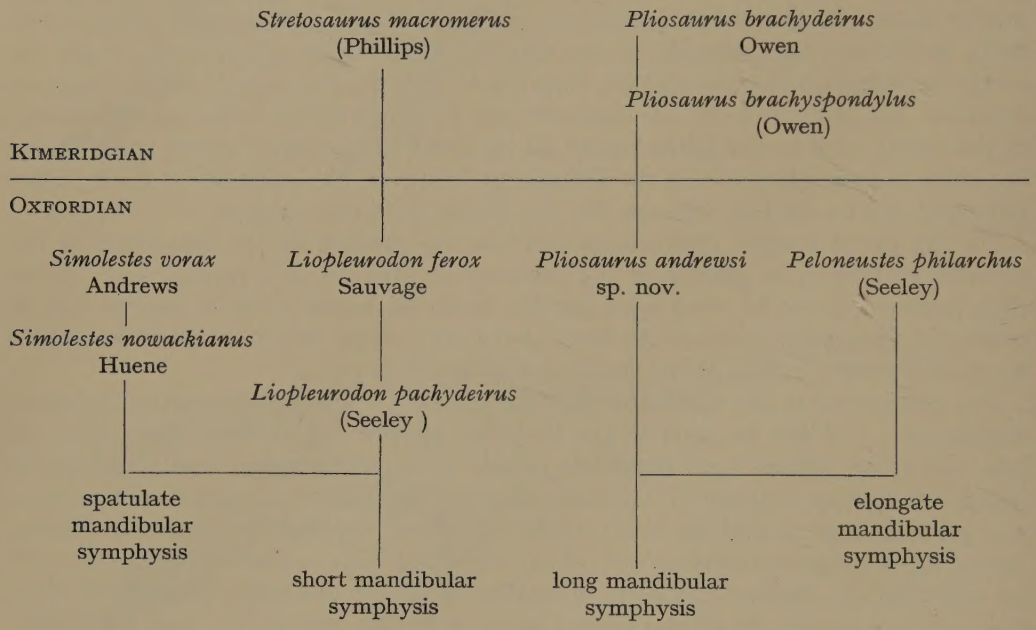

FIG. 2. Phylogeny of Upper Jurassic Pliosaur species.

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I would like to thank Dr. W. E. Swinton for his valuable help and encouragement throughout the preparation of this review, and Professor D. M. S. Watson for his very helpful criticism of the manuscript. Thanks are also due to Professor P. B. Medawar of University College, London, for the hospitality of his Department during the early stages of this work. In addition, I am pleased to acknowledge the generous assistance received from Mr. B. H. Newman of the British Museum (Nat. Hist.), Dr. C. L. Forbes of the Sedgwick Museum, Cambridge and Mr. J. M. Edmonds of the University Museum, Oxford.

Photography by Messrs. A. Barlow, W. Brackenbury, J. F. Green and A. Veenstra.

KIMERIDGIAN PLIOSAUR SPECIES

1. *Pleiosaurus aequalis* Phillips, 1871.
2. *Polyptychodon archiaci* Deslongchamps, no date (?1872).
3. *PLIOSAURUS BRACHYDEIRUS* Owen, 1841.
4. *PLIOSAURUS BRACHYSPONDYLUS* (Owen), 1839.
5. *Spondylosaurus frearsi* Fischer de Waldheim, 1845.
6. *Plesiosaurus giganteus* Conybeare, 1824*a*.
7. *Plesiosaurus grandis* Owen, 1839.
8. *Peloneustes irgisensis* Novozhilov, 1948.
9. *STRETOSAURUS MACROMERUS* (Phillips), 1871.
10. *Pleiosaurus nitidus* Phillips, 1871.
11. *Pliosaurus planus* Hulke, 1883.
12. *Pliosaurus portlandicus* Owen, 1869.
13. *Plesiosaurus recentior* Parkinson, 1822.
14. *Pliosaurus rossicus* Novozhilov, 1948.
15. *Polycotylus suprajurensis* Sauvage, 1876.
16. *Pliosaurus suprajurensis* Sauvage, 1879.
17. *Pleiosaurus simplex* Phillips, 1871.
18. *Plesiosaurus sterrodeirus* Seeley, 1869.
19. *Plesiosaurus trochanterius* Owen, 1839.
20. *Pliosaurus wosinskii* Fischer de Waldheim, 1846.

OXFORDIAN PLIOSAUR SPECIES

21. *PLIOSAURUS ANDREWSI* sp. nov.
22. *Thaumatosaurus calloviensis* Bogolubov, 1912.
23. *Pliosaurus evansi* Seeley, 1869.
24. *LIOPLEURODON FEROX* Sauvage, 1873.
25. *Pleiosaurus gamma* Phillips, 1871.
26. *Pliosaurus giganteus* Wagner, 1852.
27. *Pliosaurus giganteus* Trautschold, 1860.
28. *Liopleurodon grossouvrei* Sauvage, 1873.
29. *Ischyrodon meriani* Meyer, 1856*a*.
30. *Thaumatosaurus mosquensis* Kiprijanoff, 1883.
31. *SIMOLESTES NOWACKIANUS* Huene, 1938.
32. *Thaumatosaurus oolithicus* Meyer, 1841.
33. *LIOPLEURODON PACHYDEIRUS* (Seeley), 1869.
34. *PELONEUSTES PHILARCHUS* (Seeley), 1869.
35. *SIMOLESTES VORAX* Andrews, 1909.
36. *Sinopliosaurus weiyuanensis* Young, 1942.

N.B. The species shown in large type are here described in detail as they are considered valid.

II. SYSTEMATIC DESCRIPTIONS

Family Pliosauridae

Diagnosis. Head large, tending to be long and slender; irregular dentition with large caniniform teeth. Neck short, approximately 22 cervical vertebrae, centra short; cervical ribs double-headed. Coracoids and ischia elongated. Propodials relatively long and slender, compressed dorso-ventrally and expanded distally; humerus shorter than femur.

1. *Kimeridgian Forms*

Genus ***PLIOSAURUS*** Owen, 1841

Emended diagnosis. Mandible with long symphysis bearing 10–12 pairs of teeth of which the anterior 5–6 are large and caniniform; total of 30–38 teeth in each ramus. Cervical vertebrae short, length about half width or height; cervical ribs double-headed. Scapula triradiate with dorsal process directed laterally and ventral plate expanded medially.

Type species: *Pliosaurus brachydeirus* Owen.

Pliosaurus brachydeirus Owen

(Pl. 20; Text-figs. 3–5)

1824*a*. *Plesiosaurus giganteus* Conybeare, p. 389.
1841. *Pleiosaurus brachydeirus* Owen, pp. 282–285, pl. 68, fig. 5; pl. 72, fig. 5.
1841*a*. *Pleiosaurus brachydeirus* Owen: Owen, pp. 60–65.
1869. *Pliosaurus brachydeirus* Owen: Owen, p. 6.
1869. *Plesiosaurus sterrodeirus* Seeley, p. 98.
1871. *Pleiosaurus brachydeirus* Owen: Phillips, pp. 341–354, text-figs. 134–141, 146, 147, 160.
1879. *Pliosaurus suprajurensis* Sauvage, pp. 12–13, pl. 27, fig. 1.
1889*a*. *Pliosaurus brachydirus* Owen: Lydekker, p. 50.
1889*b*. *Pliosaurus brachydirus* Owen: Lydekker, pp. 120–128, text-figs. 36–38.
1959. *Pliosaurus brachydeirus* Owen: Delair, pp. 69–70.
1959. *Pliosaurus brachydeirus* Owen: Tarlo, pp. 286, 290.
1959*a*. *Pliosaurus brachydeirus* Owen: Tarlo, pp. 52–53.

Emended diagnosis. Teeth trihedral in cross-section, outer surface smooth and flat. Cervical vertebrae with well-marked ventral keel; posterior cervical vertebrae with boss in centre of articular surface. Epipodials short.

Material. Holotype, J.9245 A, B; J.9285; J.9292–9298; etc.; University Museum, Oxford; teeth, lower and upper jaws, vertebral column, femur, tibia, fibula; Kimeridge Clay, Market Rasen, Lincolnshire, described Owen (1841*a*), figured Phillips (1871).

History of the species. Conybeare (1824*a*) erected the name *Plesiosaurus giganteus* to cover all plesiosaurians with shortened neck vertebrae, and included in this species the pliosaur skeleton from Market Rasen, although no description of it

was given. Later, Owen (1841) described the teeth and jaws of this specimen as representing a new genus and species for which he proposed the name *Pleiosaurus brachydeirus*. The same year (1841*a*) he added a description of the vertebrae and limb bones still using the name *P. brachydeirus*, and suggested that *Plesiosaurus grandis* and *P. trochanterius* be included in the genus *Pliosaurus*.

In 1861, however, he erroneously claimed *P. grandis* as the type species of *Pliosaurus*, making *P. brachydeirus* a synonym of *P. grandis* (with the proviso in

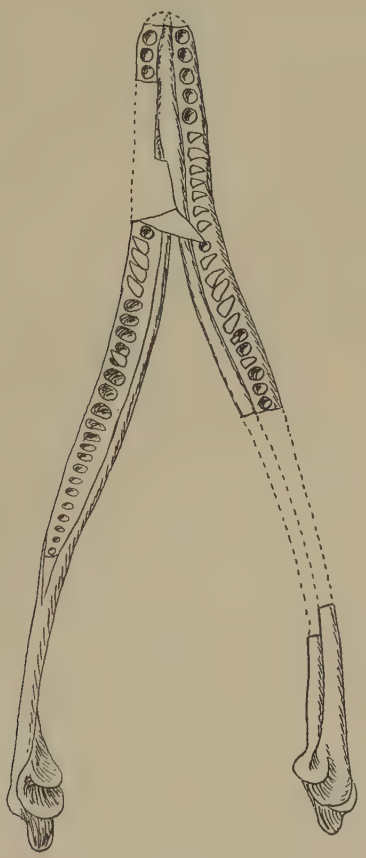


FIG. 3. *Pliosaurus brachydeirus* Owen, holotype Univ. Mus. Oxf. Mandible in dorsal view, $\times\frac{1}{10}$. After Phillips (1871).

1869 that the name *P. brachydeirus* be retained for the Market Rasen specimen). Phillips in 1871 figured the Market Rasen pliosaur under the name *P. brachydeirus*, recognizing that this was the type species. Lydekker (1889*a*, *b*) also correctly accepted *P. brachydeirus* as the type species.

Lydekker (1889*a* : 50) considered that there were 12 pairs of teeth included in the mandibular symphysis of *P. brachydeirus*, but later (1889*b* : 120, 123) he modified

his view and claimed that the symphysis only extended back to the 7th pair of teeth, the apparent length of the symphysis being due to lateral crushing. Lydekker's second view, since it appeared in the *Catalogue of Fossil Reptiles* has tended to become established, and a mandible with only 7 pairs of teeth in the symphysis is generally considered to be a diagnostic feature of the genus *Pliosaurus* (see Andrews, 1913 ; Delair, 1959). In a recent diagnosis of the genus *Pliosaurus* (Tarlo, 1959), it was claimed that 10–12 pairs of teeth in the mandibular symphysis is characteristic of the genus and in particular of the Market Rasen jaw, and the figure of the symphysial region of the mandible (Pl. 20, fig. 1) shows that there must in fact have been 10–12 pairs of teeth. A detailed description of the holotype is given below from which it is hoped that the true diagnostic features of the genus *Pliosaurus* can be established.

Description of holotype. *Teeth.* Owen (1841, pl. 68, fig. 5 ; pl. 72, fig. 5) figured the crown of a tooth belonging to the Market Rasen pliosaur. This tooth was sub-trihedral in cross-section ; the enamel of the crown was ornamented by longitudinal ridges ; the outer surface of the crown was smooth, being devoid of ridges. This flat outer surface was delimited by two strong ridges at either side, often termed carinae. (*N.B.* As all Kimeridgian pliosaurs so far described have such teeth they cannot be used to distinguish Kimeridgian species from one another.)

Mandible. The mandible (Text-fig. 3) is incomplete in the region of the symphysis and the middle portion of the right ramus is missing. The right ramus is complete up to the 12th tooth, and the left from the 12th or 13th to the 37th or 38th. It thus appears that there were 37–38 teeth in each ramus of the mandible. The three alveoli which are preserved in the anterior part of the left ramus suggest that this part of the symphysis was expanded. On the right side there are 5–7 large caniniform teeth present with their crowns missing. Posterior to these teeth are six smaller ones, all of which, with the possible exception of the last, were included in the symphysis. It appears therefore that there were 10–11 pairs of teeth in the symphysis, of which the anterior 5–7 were large and caniniform.

Vertebral column. The known vertebrae include ten cervical, twelve dorsal and one caudal. Six of the dorsal vertebrae are preserved in natural articulation with a number of fragmentary ribs and isolated teeth adhering to them. The serial position of the cervical centra can be ascertained from the fact that their length increases down the neck.

Cervical vertebrae. Five cervical vertebrae only are considered here, since the others are not well preserved. Their measurements in mm. are given in the table below :

Anterior cervical centra	Length	Width	Height
J.9292	40	88	75
J.9293	40	90	83
J.9294	42	92	85
Posterior cervical centra			
J.9297	46	110	90
J.9298	48	103	83

Anterior cervical vertebrae. The anterior articular surface is circular in outline and concave, with the margin bevelled and bordered by a narrow peripheral groove.

The margin of the posterior articular surface is bevelled in three places—between the inferior rib facets, and on either side between the superior rib facets and the base of the neural arch. On the lateral surface there are double rib facets ; the inferior facet is oval in outline (antero-posteriorly) and the superior facet tends to be triangular with a faint ridge extending from its apex to the base of the neural arch. On the ventral surface there is a strongly developed ventral keel in the mid-line, with a depression on either side. There is no suggestion of rugosity along the anterior and posterior margins.

Posterior cervical vertebrae. These centra are characterized by a large convex boss in the centre of their articular faces. The superior rib facets are larger than in the anterior cervicals and the inferior facets have usually disappeared, but specimen J.9298 has a single rib facet on its left side and a double one on the right. On the ventral surface there is no longer a ventral keel, but the centrum is strongly convex from side to side.

Dorsal vertebrae. In this part of the vertebral column the ribs are borne on the

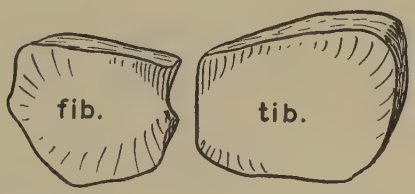


FIG. 4. *Pliosaurus brachydeirus* Owen, holotype. Epipodials of hind limb, $\times \frac{1}{5}$. fib., fibula ; tib., tibia.

transverse processes of the neural arch, and the centra are more or less cylindrical in shape but somewhat resemble a shallow pulley. Unfortunately they have no characters of diagnostic value and are useless for identification.

Caudal vertebrae. Only one centrum is known from the tail region ; it has single rib facets, and, on its anterior and posterior ventral margins, four characteristic chevron bone facets.

Limb bones. Owen (1841*a*) described two femora with different measurements in his account of the Market Rasen skeleton, but Phillips (1871) considered the smaller of the two bones to be the humerus. However, from an examination of the material, only the femur J.9285 can definitely be assigned to the type skeleton, the other probably belonging to a different animal. The length of the femur is 658 mm. and its proportions can be seen from Pl. 20, fig. 3. Preserved together with a number of tarsal bones are the tibia and fibula of the same limb as the femur (see Text-fig. 4). These two bones are of special interest as they are both much shorter than wide. Such short epipodials have previously been considered characteristic of the Cretaceous Polycotylids, so that their presence in the type of *Pliosaurus* necessitates a revision of the diagnosis of both the Pliosauridae and the Polycotylidae.

Scapula of Pliosaurus. No parts of the limb girdles of *P. brachydeirus* are known,

but in order to give a full account in one place of the diagnostic features of the genus *Pliosaurus*, a description of a scapulae of the kind belonging to *Pliosaurus brachyspondylus* is given below. This type of scapula is a triradiate bone with a strong, thickened, glenoid ramus which bears a facet for the articulation of the coracoid, and another which forms the anterior part of the glenoid cavity. Medially the scapula thins out and is expanded into a broad flat sheet termed the ventral plate. Laterally there is a further extension—the dorsal process which is approximately the same width as the glenoid ramus and which again forms a thin sheet. The dorsal process projects either laterally or postero-laterally and in ventral view is set off at an angle to the plane of the bone, from a ridge which extends to the anterior point of the ventral plate from the glenoid cavity. Immature scapulae of a similar kind are also known (Lydekker, 1889*b* : 122) but there is no way of ascertaining their specific identity. They clearly belong to *Pliosaurus* and they are of

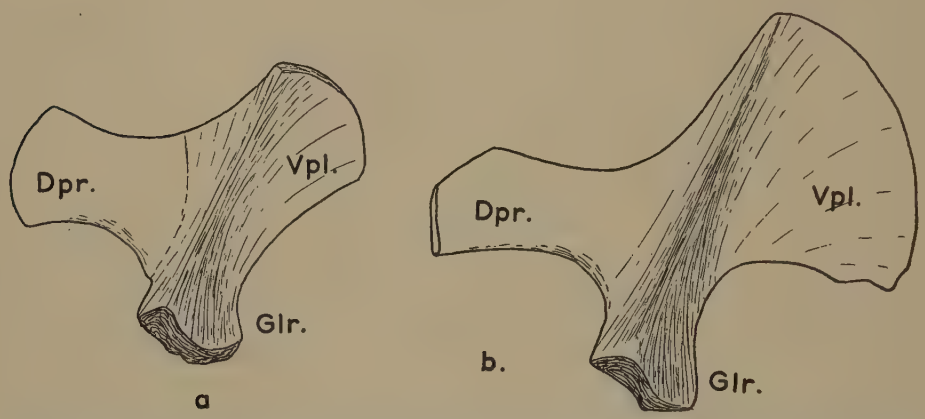


FIG. 5. *Pliosaurus* sp. Scapulae in ventral view. *a*. Immature right scapula (31934, B.M. (N.H.)) $\times \frac{1}{5}$; *b*. Adult right scapula (R.287 B.M. (N.H.)) $\times \frac{1}{8}$; Dpr., dorsal process ; Glr., glenoid ramus ; Vpl., ventral plate.

interest as they show how the proportions of the three processes of the scapula changed as the animal approached maturity. These changes can best be appreciated by comparing the immature and mature scapulae shown in Text-fig. 5.

Pliosaurus brachyspondylus (Owen)

(Pl. 21 ; Text-fig. 6)

1822. *Plesiosaurus recentior* Parkinson, pp. 295–298.
1824*a*. *Plesiosaurus giganteus* Conybeare, p. 389.
1839. *Plesiosaurus brachyspondylus* Owen, pp. 78–80.
1845. *Plesiosaurus brachyspondylus* Owen : Owen, p. 417.
1845. *Spondylosaurus frearsi* Fischer de Waldheim, pp. 343–351, pls. 7, 8.
1846. *Pliosaurus wosinskii* Fischer de Waldheim, pp. 90–107, pls. 3, 4.
1868. *Pliosaurus brachyspondylus* (Owen) Eichwald, pp. 1280–1281.

1869. *Pliosaurus brachyspondylus* (Owen) : Seeley, pp. 97, 102–104.
1871. *Pleiosaurus nitidus* Phillips, pp. 360–361, text-figs. 156–158.
1889*b*. *Pliosaurus brachyspondylus* (Owen) : Lydekker, pp. 139–140.
1959. *Pliosaurus brachyspondylus* (Owen) : Tarlo, pp. 283–291, text-figs. 1, 2, pls. 51, 52.
1959. *Pliosaurus brachyspondylus* (Owen) : Delair, pp. 70–71.

EMENDED DIAGNOSIS. Teeth trihedral in cross-section, outer surface smooth and flat. Cervical vertebrae with finely sculptured double rugosity on ventral surface and no ventral keel ; posterior cervical vertebrae with no boss in centre of articular surfaces.

MATERIAL. Proposed Neotype, J.29564, Sedgwick Museum, Cambridge ; posterior cervical centrum ; Kimeridge Clay, Ely, Cambridgeshire ; described Seeley (1869 : 97, 103), figured Tarlo (1959, pl. 51, figs. 1–1*c*). For list of other material, see Tarlo (1959).

HISTORY OF THE SPECIES. In 1822 Conybeare read a paper (1824) to the Geological Society of London in which he figured several pliosaur neck vertebrae from the Kimeridge Clay of Weymouth. Also in 1822, Parkinson assigned all such vertebrae to the species *Plesiosaurus recentior*. Conybeare later (1824*a*) proposed the name *Plesiosaurus giganteus* for plesiosaurians with shortened neck vertebrae and included the remains from Weymouth in this species. Owen (1839) also described such shortened cervical vertebrae from the Kimeridge Clay of the Headington Pits near Oxford, but proposed the name *Plesiosaurus brachyspondylus* for them and also for the vertebrae from Weymouth. This specific name was in fact the first that could be considered valid since it was accompanied by an adequate description. He later (1845) identified a cervical centrum from the Kimeridge Clay of Moscow as belonging to the same species, although Fischer de Waldheim (1845) made it the type of the species *Spondylosaurus frearsi*. Unfortunately the specimens from Headington, formerly in the collection of Viscount Cole (later Earl of Enniskillen) can no longer be traced, and those from Weymouth were destroyed during the bombing of Bristol in November 1940 (Swinton, 1948 ; Delair, 1959).

Seeley (1869) was the only other author to discuss the species *Plesiosaurus brachyspondylus* which he correctly assigned to the genus *Pliosaurus*, following Eichwald (1868). In his paper Seeley described a posterior cervical centrum from the Kimeridge Clay of Roswell Pit, near Ely, as *Pliosaurus brachyspondylus* and this specimen has recently been proposed as the neotype (Tarlo, 1959).

It should be noted that Phillips (1871) described and figured several plesiosaur vertebrae and incorrectly assigned them to *Plesiosaurus brachyspondylus* Owen. In the same work he figured a posterior cervical centrum which he named *Pleiosaurus nitidus*. This specimen is now lost but Lydekker (1889*b*) claimed that it closely accorded with the posterior cervical centrum described by Seeley (1869) as belonging to *P. brachyspondylus*. Phillips' figure supports Lydekker's view and thus *P. nitidus* is here included as a synonym of *P. brachyspondylus*.

In 1889 a pliosaur skeleton was discovered in the Kimeridge Clay of Roswell Pit near Ely, and it has been recently described and figured (Tarlo, 1959) under the name *Pliosaurus brachyspondylus* (Owen). This pliosaur skeleton is the most com-

plete of any from the Kimeridge Clay. This species, which was formerly one of the most obscure, is now the best known of Kimeridgian pliosaurs.

DESCRIPTION OF PROPOSED NEOTYPE. The neotype centrum is very distinctive as it possesses a double rib facet on its left side and a single facet on the right. The articular surfaces of the vertebra are transversely ovate in outline and are slightly concave. Each has a small depression at its centre, without any suggestion of convexity here as in the posterior cervical vertebrae of other Kimeridgian pliosaur species. The margins of the articular surfaces are very sharply defined, and there is no evidence of either a marginal bevel or groove. On the anterior and posterior margins

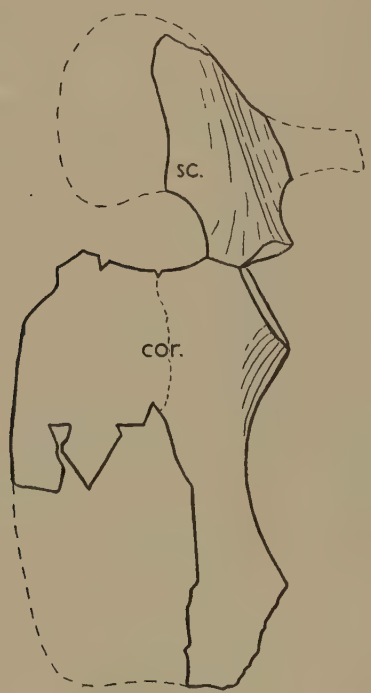


FIG. 6. *Pliosaurus brachyspondylus* (Owen). J.35991, Sedgwick Mus. Reconstruction of left half of pectoral girdle, $\times \frac{1}{8}$. After Tarlo (1959.)

of the ventral surface of the centrum are two strips of finely sculptured rugose bone between which the surface is remarkably smooth. This last feature is very striking and can readily be used to distinguish the species.

DESCRIPTION OF ASSOCIATED SKELETON FROM ELY. *Teeth.* The teeth are similar to those of *Pliosaurus brachydeirus* Owen, being trihedral in cross-section; the enamel of the flat outer surface is smooth but the remainder of the crown is characterized by longitudinal ridges.

Mandible. The symphysial portion of the mandible contains 10 teeth on each side, of which the anterior six are large and caniniform. There are 30 teeth in the right ramus and 31 in the left. This specimen is similar in shape to the mandible of *P. brachydeirus*.

Cervical vertebrae. The first cervical vertebra posterior to the atlas-axis has a pronounced ventral lip directed anteriorly with a marked rugose area behind it on the ventral surface of the centrum, which tends to produce a faint ventral keel. However, in the majority of the cervical vertebrae, there is no suggestion of such a keel, and the rugosities on their ventral surfaces are limited to strips along the anterior and posterior margins. There are double rib facets on the lateral surfaces of the centra of all the anterior cervical vertebrae, the inferior facet in each case being more or less circular in outline, while the superior facet tends to be triangular with a narrow ridge extending from its apex to the base of the neural arch. The articular surfaces of the anterior cervicals show a well-developed marginal bevel, but this disappears in the posterior cervicals. The articular surfaces are also slightly concave and have a small central pit, no mamilla being developed as in other Kimeridgian species.

The four most posterior of the cervical centra can be distinguished from the anterior cervicals because they have single rib facets, and the bevelling of the margins of their articular surfaces is slight. The articular surfaces are slightly concave and each has a depression in the centre, but the boss usually found in Kimeridgian species is absent. In other respects the posterior cervical vertebrae resemble the anterior cervicals.

Scapula. Sufficient of the left scapula is preserved in one piece on the ventral surface of a series of vertebrae to show that it is of the same kind as that described above under *P. brachydeirus*, and a reconstruction of this bone is given in Text-fig. 6 together with that of the coracoid.

Propodials. The humerus is completely preserved and is indistinguishable from the propodials of most other pliosaurs. The left femur is also preserved whole with a number of phalanges adhering to it. This bone although larger is very similar to the humerus in its proportions.

Epipodials. No epipodials are known from this skeleton.

Genus ***STRETOSAURUS*** Tarlo, 1959

Diagnosis. Mandible with short symphysis bearing 5–6 pairs of large caniniform teeth ; total of approximately 24–26 teeth in each ramus. Teeth trihedral in cross-section, outer surface smooth and flat. Cervical vertebrae short, length less than half width or height. ventral keel absent ; posterior cervical vertebrae with rib facets borne on pedicle and boss in centre of articular surfaces. Caudal vertebrae with no chevron bone facets. Scapula triradiate with dorsal process produced anteriorly and ventral plate little expanded. Epipodials short.

Type species : *Stretosaurus macromerus* (Phillips)

Stretosaurus macromerus (Phillips)

(Pl. 22 ; Text-figs. 7, 8)

1869. *Pliosaurus grandis* (Owen) : Owen, pp. 1–6, pls. 1, 2.
1869*a*. *Pliosaurus grandis* (Owen) : Owen, pp. 152–153, pl. 18.
1869. *Pliosaurus brachydeirus* Owen : Seeley, pp. 102–104.
1869. *Pliosaurus grandis* (Owen) : P. Fischer, pp. 253–269, pl. 15.
1871. *Pleiosaurus macromerus* Phillips, pp. 354–358, text-figs. 148, 151, 159.
1872?. *Polyptychodon archiaci* Deslongchamps, pp. 30–35, pl. 5, figs. 1, 2 ; pl. 11, figs. 5, 6.
1889*b*. *Pliosaurus macromerus* Phillips : Lydekker, pp. 131–139, text-figs. 41–43.
1947. *Pliosaurus* cf. *grandis* (Owen) : Rozhdestvensky, pp. 197–199, text-figs. 1, 2.
1958*a*. *Pliosaurus macromerus* Phillips : Tarlo, pp. 193–199, text-figs. 1*c*, 2*b* 3, 4 ; pls. 36, 37.
1959. *Pliosaurus macromerus* Phillips : Delair, pp. 71–72.
1959*a*. *Stretosaurus macromerus* (Phillips) Tarlo, pp. 39–55, text-figs. 1–6, pls. 7–9.

Diagnosis. As for genus (only species).

Material. Lectotype, J.10441, University Museum, Oxford ; anterior cervical centrum ; Kimeridge Clay, Shotover Railway Cutting, Oxfordshire. Figured Phillips (1871, fig. 148), Tarlo (1959*a*, pl. 8, figs. 1–1*b*). For other material see Tarlo (1959*a*).

History of the species. Owen described and figured a cervical centrum from the Kimeridge Clay of Foxcombe Hill, near Oxford, under the name *Pliosaurus grandis* (1869*a* : 152–158, pl. 18, figs. 1, 2). This specimen accords with the lectotype of *Stretosaurus macromerus* (Phillips) being notable for the absence of a ventral keel. At the same time Owen (1869) also described and figured a large mandible from the Kimeridge Clay of Kimeridge Bay as *P. grandis*. Its mandible contained 25–26 pairs of teeth of which the anterior six pairs were large and caniniform, these forming the full complement of teeth in the symphysis. P. Fischer (1869) described and figured a similar type of mandible from the Kimeridge Clay of Le Havre. Deslongchamps (?1872), described the same specimen under the name *Polyptychodon archiaci*, but his figures are the mirror-images of those of P. Fischer. Recently a similar mandible of giant size from the Kimeridge Clay of Cumnor was described and figured (Tarlo, 1959*a*) when all Kimeridgian mandibles with this comparatively short mandibular symphysis were provisionally assigned to *Stretosaurus macromerus*.

Seeley (1869) described some posterior cervical vertebrae under the name *Pliosaurus brachydeirus* and these have recently been referred to *S. macromerus* (see Tarlo, 1959*a*). Phillips (1871) erected the name *Pleiosaurus macromerus* to cover a miscellaneous collection of vertebrae and a large propodial bone. The anterior cervical centrum which he figured (fig. 148) has been chosen as the lectotype. Lydekker (1889*b*) placed most pliosaur remains of large size in *P. macromerus* including the mandible described by Owen (1869). Tarlo (1958*a*) described the scapula of *P. macromerus* and later (1959*a*) claimed that the pectoral girdle was sufficiently distinct from that of *Pliosaurus* to warrant the erection of the new genus *Stretosaurus*.

It should be noted, however, that although Kuhn (1935) lists " *Plesiosaurus macromerus* Giebel, 1847 " in his synonymy of the species this is actually incorrect

as Giebel (1847) listed Owen's species *Plesiosaurus macromus* which is in no way connected with *S. macromerus*.

Description of Lectotype. The lateral surface of the lectotype centrum bears two rib facets which are oval in outline, their long axes being directed antero-posteriorly. In this specimen the superior facet is smaller than the inferior. The

Fig. 7. *Stretosaurus macromerus* (Phillips). J.35990, Sedgwick Mus. Left femur in ventral view, $\times \frac{1}{3}$.

lateral surface between the base of the neural arch and the superior rib facet is quite smooth with no suggestion of a ridge. The anterior articular surface is concave with a poorly developed mamilla at the centre; the outline of the centrum is circular with a well-marked peripheral groove. The posterior articular surface is also concave and somewhat circular in outline, with its margin bevelled along the ventral edge and also between the base of the neural arch and the top of the rib facets. The

anterior and posterior margins of the ventral surface of the centrum are somewhat roughened; there is no evidence of a ventral keel.

Description of associated skeleton from Stretham. *Teeth.* The teeth are similar to those of *Pliosaurus brachydeirus* Owen, being trihedral in cross-section; the enamel of the flat outer surface is smooth but the remainder of the crown is characterized by longitudinal ridges.

Cervical vertebrae. The ventral surface of the four known anterior cervical vertebrae is flat with no suggestion of a ventral keel; the lateral surface of the centra between the superior rib facet and the neural arch is smooth with no indication of a ridge. In the centre of each articular surface a small mamilla is found punctured by a nutritive foramen. Three centra are known from the posterior part of the neck.

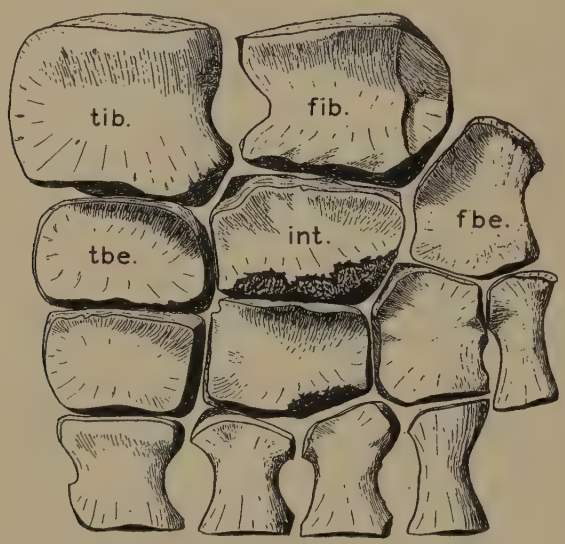


Fig. 8. *Stretosaurus macromerus* (Phillips). J.35990, Sedgwick Mus. Epipodials and tarsus of left hind limb, in dorsal view, $\times\frac{1}{6}$. tib., tibia; fib., fibula; tbe., tibiale; int., intermedium; fbe., fibulare.

All have a large rounded boss in the centre of their articular surfaces, and compared with the anterior cervicals the first two specimens show a marked reduction of the inferior rib facets. In the last posterior cervical centrum only a single rib facet remains. this being borne on a pedicle situated on the upper half of the lateral surface of the centrum. A sharp ridge is developed between the dorsal edge of this pedicle and the base of the neural arch, the suture line of which extends laterally towards the rib facet.

Scapula. The scapula is a triradiate bone in which the whole surface is in one plane, no part being set off at an angle. The glenoid ramus is thickened and elongated, the ventral plate is not greatly expanded, and the dorsal process is produced anteriorly and does not project laterally. By the anterior production of the dorsal

process of the scapula the pre-glenoid length of the whole pectoral girdle is greatly increased. A pectoral girdle containing the type of scapula described above is different from that of any previously known pliosaur, and for this reason the new genus *Stretosaurus* was proposed.

Propodials. The head of the humerus is more massive than that of the femur although the humerus is, on the whole, a smaller bone with a very slender shaft; the femur has more normal proportions (see Text-fig. 7).

Epipodials. These are short as in *Pliosaurus brachydeirus* (Text-fig. 8).

Description of mandible of *Stretosaurus*. No mandible is known from *Stretosaurus macromerus*, but a description is given below of the kind of mandible generally assigned to this species. There are usually 25 pairs of teeth in the mandible, but only the anterior 6–7 pairs, which are large and caniniform, are included in the symphysis. This type of mandible contrasts with that of *Pliosaurus* where there are 10–12 pairs of teeth in the symphysial portion.

2. *Oxfordian Forms*

Genus ***PLIOSAURUS*** Owen, 1841

Pliosaurus andrewsi sp. nov.

(Pl. 23; Pl. 28; figs. 4–4*b*)

1871. *Pleiosaurus ? grandis* (Owen) : Phillips, p. 318, text-fig. 122.
1889*b*. *Pliosaurus evansi* Seeley : Lydekker, p. 129.
1889*b*. *Pliosaurus grossouvrei* (Sauvage) Lydekker, pp. 130–131, text-fig. 40.
1889*b*. *Peloneustes philarchus* (Seeley) : Lydekker, p. 154.
1890. *Peloneustes evansi* (Seeley) Lydekker, pp. 49–52.
1890*a*. *Peloneustes evansi* (Seeley) : Lydekker, p. 273.
1913. *Peloneustes evansi* (Seeley) : Andrews, pp. 71–79, text-figs. 6B, 27B, 28–30.
1946. ?*Sinopliosaurus weiyuanensis* Young : Young, pp. 203–205, pl. 2, fig. 3*b*.
1958. *Pliosaurus* sp. nov. Tarlo, pp. 439–441.

Diagnosis. Teeth circular in cross-section; enamel smooth with few fine ridges mainly confined to inner surface of crown. Cervical vertebrae generally have no ventral keel; no finely sculptured double rugosities present on ventral surface. Epipodials long.

Material. Holotype, R.3891, British Museum (Nat. Hist.), associated skeleton, Oxford Clay, Peterborough, figured Andrews (1913).

History of the species. Phillips (1871) figured a mandible from the Oxford Clay of Eyebury, under the name *Pleiosaurus ?grandis*. As this specimen has a mandibular symphysis containing 11 pairs of teeth, of which the anterior 5–6 are large and caniniform, Lydekker (1889a) referred it to *Peloneustes philarchus* (Seeley). At the same time he described a number of teeth of Corallian age under the name *Pliosaurus grossouvrei* (Sauvage) commenting that they might in fact belong to

P. evansi. Lydekker (1890, 1890*a*) included the same mandible in *Peloneustes evansi* (Seeley). In 1913 Andrews described an associated pliosaur skeleton under the name *Peloneustes evansi* which had a similar mandible, and since the mandible of this species is much like that of *Pliosaurus brachydeirus* (the type species) it should be placed within the genus *Pliosaurus*. However, the material described by Lydekker and Andrews as *P. evansi* is unlike Seeley's type of this species (which in any case is now included in the synonymy of *Peloneustes philarchus*) and a new species *Pliosaurus andrewsi* is here proposed for this material. The skeleton described by Andrews is chosen as the holotype of this new species. Young (1946) described several teeth which he referred to *Sinopliosaurus weiyuanensis*, but from their description they appear to be conspecific with *P. andrewsi*.

Description of holotype. *Teeth*. The teeth are circular in cross-section ; the enamel of the crown is generally smooth, the few enamel ridges being confined to the inner surfaces. This pattern of ornamentation is very distinctive and enables the species to be recognized from isolated teeth. A feature of the teeth of this species, noted by Andrews, is that they undergo wear to a greater extent than in any other plesiosaurian.

Mandible. Unlike the mandible figured by Phillips (1871), the specimen has been crushed laterally. The slight angle in the two rami (at the 12th tooth) marks the end of the symphysis which contained 12 pairs of teeth, the anterior seven of which were large and caniniform. The total number of teeth in each ramus was about 32. This mandible is very similar to that of *P. brachydeirus*.

Vertebral column. The entire vertebral column is preserved, but as the dorsal and caudal vertebrae add little to our knowledge their description is omitted. The cervical vertebrae are, however, of critical importance, as it was by means of their characters only that this skeleton was incorrectly placed in the species *Peloneustes evansi* by Andrews.

Cervical vertebrae. The articular surfaces are circular in outline with a narrow peripheral groove. In this skeleton the double-headed cervical ribs are preserved in natural articulation. The most important feature of these vertebrae is, however, the complete absence of a ventral keel, quite unlike the type specimen of *P. evansi* (now referred to *Peloneustes philarchus*) in which the ventral keel is strongly developed. On the lateral surface of the centra there is no ridge between the superior rib facet and the base of the neural arch. One of the posterior cervical centra is of interest since it exhibits a double rib facet on the left side and a single one on the right. Isolated vertebrae of this species are virtually indistinguishable from those of *Simolestes vorax* Andrews.

Propodials. Both hind and fore limbs are preserved. The humerus is shorter and broader than the femur.

Epipodials. The tibia, fibula and ulna are greater in length than in width ; in the radius, however, these proportions are reversed.

Scapula of P. andrewsi. There is no scapula associated with the holotype but the skeleton (R.2437) which can be referred to *Pliosaurus andrewsi* contains a scapula. It is similar to that described under *P. brachydeirus*, except that the dorsal process is somewhat expanded distally (see Pl. 23, fig. 1).

Genus *LIOPLEURODON* Sauvage, 1873

EMENDED DIAGNOSIS. Mandible with short symphysis bearing 5–7 pairs of large caniniform teeth ; total of about 25–28 teeth in each ramus. Teeth circular in cross-section ; fewer longitudinal ridges on outer surface of crown than on inner surface. Cervical vertebrae short, length half or less than half of width or height. Scapula triradiate with dorsal process directed laterally and ventral plate expanded medially. Epipodials long.

TYPE SPECIES : *Liopleurodon ferox* Sauvage.

Liopleurodon ferox Sauvage

(Pl. 24 ; Pl. 28, figs. 2–2*b*)

1852. *Pliosaurus giganteus* Wagner, pp. 663–710, pl. 20.
1856.*a* *?Ischyrodon meriani* von Meyer, pp. 19–21, pl. 2, figs. 1–4.
1860. *Pliosaurus giganteus* Trautschold, p. 356, pl. 8, fig. 25.
1873. *Liopleurodon ferox* Sauvage, pp. 378–379, pl. 7, fig. 1.
1880. *Polyptychodon ferox* (Sauvage) Sauvage, p. 544.
1883. *Thaumatosaurus mosquensis* Kiprijanoff, p. 27, pl. 14, fig. 1.
1888. *Pliosaurus ferox* (Sauvage) Lydekker, p. 353.
1889*b*. *Pliosaurus ferox* (Sauvage) : Lydekker, pp. 145–147, text-fig. 45.
1897. *Pliosaurus ferox* (Sauvage) : Andrews, pp. 177–183, pl. 12.
1905. *Liopleurodon ferox* Sauvage : Blake, pp. 23–25.
1911. *Pliosaurus* (*Liopleurodon*) cf. *ferox* (Sauvage) : Bogolubov, pp. 153–154.
1912. *Liopleurodon ferox* Sauvage : Bogolubov, p. 5.
1913. *Pliosaurus ferox* (Sauvage) : Andrews, pp. 2–23, text-figs. 2, 3, 7 ; pls. 1, 2.
1934. *Pliosaurus ferox* (Sauvage) : von Huene, pp. 31–46, text-figs. 1–26.
1939. *Pliosaurus* cf. *ferox* (Sauvage) : Bigot, pp. 635–636, pl. 37 *bis*.
1944. *Pliosaurus ferox* (Sauvage) : Gross, pp. 227–230, text-figs. 1–3.

EMENDED DIAGNOSIS. Teeth with ornamentation of well-spaced coarse ridges on inner surface, and few widely and unevenly spaced ridges on outer surface between which are wide smooth areas. Cervical vertebrae with length less than half width or height ; ventral lip developed on anterior surface of centrum, ventral keel absent.

MATERIAL. Holotype, a tooth from the Oxford Clay of Wast near Boulogne. Associated skeleton (R.3536) from the Oxford Clay of Peterborough.

HISTORY OF THE SPECIES. In 1852, Wagner described and figured a tooth from the Oxfordian of Bavaria under the name *Pliosaurus giganteus* ; this tooth was circular in cross-section, and thus differed from all other pliosaur remains described at that time (with the exception of *Thaumatosaurus oolithicus* Meyer). Unfortunately Wagner's trivial name had been used by Conybeare (1824*a*) for pliosaur remains which he named *Plesiosaurus giganteus*. Meyer (1856*a*) described and figured a further tooth of Oxfordian age with a circular cross-section to which he gave the name *Ischyrodon meriani*. (He had erected this name in 1838, but it remained a *nomen nudum* until 1856*a*.) Although this tooth has generally been included in the synonymy of the Kimeridgian *S. macromerus* (see Lydekker, 1889*b* ; Delair, 1959), it is suggested

here that it may belong to *L. ferox* Sauvage. It is not certain from Meyer's figure whether this assignment is altogether justified, but it is closer to *L. ferox* than to any other species and is therefore tentatively included in its synonymy. Trautschold (1860) described and figured a small tooth of Oxfordian age under the preoccupied name of *Pliosaurus giganteus.*

Sauvage (1873) described a tooth from the Oxford Clay of Wast near Boulogne-sur-Mer, which he made the type of *Liopleurodon ferox.* In 1880 he transferred this species to the genus *Polyptychodon.* Lydekker (1888) referred the species to *Pliosaurus* and described some Oxfordian pliosaur remains under the name *Pliosaurus ferox.* These are referred below to *Liopleurodon pachydeirus* (Seeley).

Blake (1905) discussed the generic name, arguing for the retention of Sauvage's name *Liopleurodon.* Bogolubov (1911) retained it, but only as a subgenus of *Pliosaurus* ; but later (1912), he too accepted *Liopleurodon* as the generic name for *L. ferox.* All subsequent authors have taken *Liopleurodon* to be a synonym of *Pliosaurus* (Andrews, 1913 ; Linder, 1913 ; Delair, 1959). It is clear, however, that *L. ferox,* which has a mandible with a short symphysis containing 6–7 pairs of large caniniform teeth is distinct from *Pliosaurus,* and should be generically distinguished from it. For this reason I have followed Blake and resurrected Sauvage's original generic name *Liopleurodon.* The re-description given below is based on the associated skeleton (R.3536) which has teeth identical in character with the holotype. It is considered necessary to include it here as even Andrews' excellent description of this species (1913) suffered from the inclusion of material which I have felt obliged to transfer to *L. pachydeirus* (Seeley). The skeleton described as *Pliosaurus ferox* by von Huene (1934) is retained in that species on the characters of its teeth. The teeth described by Bigot (1939) are also referable to *L. ferox.*

Description of holotype. Sauvage's description of the holotype tooth (1873 : 379) repeated by Andrews (1913 : 10–11) leaves little to be added. The longitudinal ridges of the crown are coarse and on the external surface are unevenly spaced, with wide smooth areas between them.

Description of associated skeleton from Peterborough. *Teeth.* Indistinguishable from the type described and figured by Sauvage (1873).

Mandible. There are 24 alveoli present in the left ramus, and there were also probably 24 in the right. There are six pairs of large caniniform teeth in the symphysis and the mandible is somewhat expanded to accommodate them. The seventh tooth is greatly reduced, and from about the eleventh tooth, the teeth gradually diminish in size.

Cervical vertebrae. Andrews (1913, text-fig. 2), figured a cervical vertebra of this skeleton, but it is given a detailed description here as it is important in the specific diagnosis of this form. The anterior articular surface is somewhat heart-shaped in outline, with the ventral margin produced to form a small " v " in the mid-line. The surface is concave with a deep pit at the centre, no mamilla being developed. The margins are gently bevelled and are sharply delimited by a continuous peripheral groove. The posterior articular surface is similar to the anterior but the margin is strongly bevelled in the ventral quadrant so that it appears to be folded over on to the ventral surface of the centrum. In ventral view the centrum is produced ante-

riorly in the mid-line to form a ventral lip which in anterior view is cut off by the peripheral groove. There is no ventral keel in the mid-line.

Scapula. The scapula (Pl. 24, fig. 3) is poorly preserved, but it shows the kind possessed by the genus *Liopleurodon*. The short stout glenoid ramus bears an articular facet for the coracoid, and in ventral view a ridge can be observed extending from the glenoid cavity anteriorly. The narrow dorsal process which is directed posterolaterally is set off from the plane of the rest of the bone by this ridge.

Propodials. The femur is figured (Pl. 24, fig. 4) for the first time. It is of special interest as it has almost parallel sides for the greater part of its length. Its distal articular surface also shows a well-marked facet for a pisiform bone in addition to the normal articular facets. This is worthy of mention as it has generally been believed that such pisiform bones were not present until Cretaceous times.

Epipodials. The tibia and fibula are considerably longer than wide.

Liopleurodon pachydeirus (Seeley)

(Pl. 25 ; Pl. 28, figs. 1–1*b*)

1869. *Pliosaurus pachydeirus* Seeley, p. 118.
1888. *Pliosaurus ferox* (Sauvage) : Lydekker, p. 353.
1889*b*. *Pliosaurus ferox* (Sauvage) : Lydekker, pp. 145–147.
1890. *Pliosaurus ferox* (Sauvage) : Lydekker, pp. 49–52, pl. 5.
1905. *Liopleurodon ferox* Sauvage : Blake, pp. 23–25, pl. 1, figs. 1, 2.
1913. *Pliosaurus ferox* (Sauvage) : Linder, pp. 375–390, text-figs. 24–32 ; pl. 35, figs. 3–8.
1913. *Pliosaurus ferox* (Sauvage) : Andrews, pp. 23–24, text-figs. 4, 6A.
1949. *Pliosaurus* cf. *ferox* (Sauvage) : Follet, pp. 22–24, text-fig. 1.
1958. *Pliosaurus pachydeirus* Seeley : Tarlo, pp. 440–441.

DIAGNOSIS. Teeth with fine closely packed enamel ridges on inner surface and 6–8 evenly spaced ridges on outer surface. Cervical vertebrae with length about half width or height, with faint ventral keel.

MATERIAL. Holotype, a series of associated cervical vertebrae (J.46912), Sedgwick Museum, Cambridge, from Oxford Clay of Great Gransden. Associated skeleton R.2446, British Museum (Nat. Hist.), described and figured Lydekker (1890).

HISTORY OF THE SPECIES. Seeley (1869 : 118) listed an atlas and axis together with fifteen cervical vertebrae from the Oxford Clay of Great Gransden, which he named *Pliosaurus pachydeirus*, but since he gave no description of them the name was invalid. These vertebrae were included in the species *P. ferox* by Lydekker (1888, 1889*b*). Lydekker (1890) described and figured an Oxfordian pliosaur skeleton under the name *Pliosaurus ferox* (Sauvage) as its cervical vertebrae resembled the " associated series to which Professor Seeley applied the name of *Pliosaurus pachydeirus* ", but he recognized that its teeth differed from the type of *L. ferox* in that the " intercarinal space " was " scarcely definable " and the longitudinal ridges of the enamel were rather more " continuous and closer together ". Blake (1905) described similar teeth under the name *Liopleurodon ferox*, recognizing that they

were similar to those described by Lydekker (1890). In 1913 Andrews correctly described as *P. ferox* part of an Oxfordian pliosaur skeleton which had teeth indistinguishable from Sauvage's type tooth, but with cervical vertebrae quite different from those figured by Lydekker (1890) as *P. ferox*. These two skeletons, which are re-described here, are obviously closely related, but as they differ in the characters of their teeth and cervical vertebrae I consider them to be specifically distinct, and am assigning the material described by Lydekker (1890) to Seeley's species which thus becomes *Liopleurodon pachydeirus* (Seeley). The skeleton described as *Pliosaurus ferox* by Linder (1913) is referable to *L. pachydeirus* on the characters of its cervical vertebrae.

Description of holotype. The cervical vertebrae listed by Seeley (1869) are described and figured here for the first time. These cervical vertebrae are similar to those of *L. ferox*, but can be distinguished from them as they are proportionately greater in length, possess a faint ventral keel, but have no ventral lip. The measurements in mm. of some of the type centra are given in the following table :

Cervical centra	Length	Width	Height
J.46912 1	45	96	87
„ 2	46	97	88
„ 3	47	99	88
„ 4	48	104	93
„ 5	49	109	97
„ 6	50	115	102

Description of associated skeletons from Peterborough. *Teeth.* These are all circular in cross-section. The longitudinal ridges on the enamel of the crown are finer and more closely packed on the internal surface than in *L. ferox*. On the outer convex surface there are approximately 6–8 evenly spaced ridges. In this latter feature these teeth contrast markedly with those of *L. ferox*.

Mandible. According to Lydekker (1890 : 50) the mandibular symphysis extends back to the seventh tooth, but the only part of the mandible now known is that figured in Pl. 6, fig. 3 which bears 3–4 pairs of large caniniform teeth posterior to which the symphysis ends. All the teeth in the symphysis were large and caniniform and no series of smaller teeth was included in it as in *P. brachydeirus*. Thus in this feature *L. pachydeirus* is indistinguishable from *L. ferox*, and can be included in the same genus—*Liopleurodon*.

Cervical vertebrae. The cervical vertebrae described by Lydekker (1890) accord well with the type and are easily distinguished from *L. ferox* by their comparatively greater length and faint ventral keel.

Propodials. The femur is known and was figured, together with the tibia and fibula, by Andrews (1913) as *P. ferox*. If the femora of *L. pachydeirus* and *L. ferox* are compared, it can be seen that their proportions are very different. Although generally one cannot differentiate species on propodials, in this case it appears possible.

Epipodials. The tibia and fibula are longer than they are wide, as in other Oxfordian pliosaur species.

Genus *PELONEUSTES* Lydekker, 1889

EMENDED DIAGNOSIS. Mandible with very long symphysis bearing 13–14 pairs of teeth, of which the anterior 6–7 are large and caniniform ; total of about 40 teeth in each ramus. Teeth circular in section ; the majority of longitudinal enamel ridges reach half-way up the crown, relatively few continuing to the tip. Cervical vertebrae short, length slightly more than half the width or height ; well-marked ventral keel. Scapula triradiate with dorsal process directed laterally and ventral plate expanded medially. Epipodials long.

TYPE SPECIES : *Peloneustes philarchus* (Seeley).

Peloneustes philarchus (Seeley)

(Pl. 26 ; Text-fig. 9)

1869. *Plesiosaurus philarchus* Seeley, pp. 139–140.
1869. *Pliosaurus evansi* Seeley, pp. 116–117.
1877. *Pliosaurus evansi* Seeley : Seeley, pp. 716–723, text-figs. 1–9.
1888. *Thaumatosaurus philarchus* (Seeley) Lydekker, pp. 352–353.
1889. *Peloneustes philarchus* (Seeley) Lydekker, pp. 49–50, text-fig. 1A.
1889*a*. *Peloneustes philarchus* (Seeley) : Lydekker, pp. 48–56, text-figs. 4–9, pl. 2.
1889*b*. *Peloneustes philarchus* (Seeley) : Lydekker, pp. 151–152, 154–158, text-figs. 47A, 48, 49, 51–55.
1892. *Pliosaurus philarchus* (Seeley) Seeley, p. 127.
1908. *Peloneustes philarchus* (Seeley) : Jaccard, pp. 395–398, pls. 26–32.
1913. *Peloneustes philarchus* (Seeley) : Linder, pp. 341–367, 369–375 ; text-figs. 1–21 ; pls. 33, 34, 35, figs. 1, 2.
1913. *Peloneustes philarchus* var. *spatyrhynchus* Linder, pp. 368–369, text-figs. 22–23.
1913. *Peloneustes philarchus* (Seeley) : Andrews, pp. 34–70, 202, text-figs. 11–26, 27A ; pl. 4.

DIAGNOSIS. As for genus (only species).

MATERIAL. Holotype, J.46913, Sedgwick Museum, Cambridge, associated skeleton from Oxford Clay of Peterborough.

HISTORY OF THE SPECIES. Seeley (1869 : 139–140) gave a brief description of an associated pliosaur skeleton from the Oxford Clay of Peterborough which he named *Plesiosaurus philarchus*. In 1888 Lydekker transferred the species to Meyer's genus *Thaumatosaurus*. Lydekker (1889*a*) described further material of the same species and proposed the new generic name *Peloneustes*. Later, (1889*b*) he figured a cervical centrum and, in his diagnosis of the genus *Peloneustes* he claimed that the cervical centra were " without a haemal ridge " (ventral keel), although his figure gives no evidence either way. This last point is of some importance, since in fact the cervical vertebrae of *Peloneustes philarchus* have a well-marked ventral keel and are distinguished from those of *Pliosaurus andrewsi* by its presence.

Seeley (1892) claimed that the species *P. philarchus* could not be generically

separated from *Pliosaurus*, but though it is evident that it is somewhat like *Pliosaurus brachydeirus* in the character of the mandibular symphysis, since the name *Peloneustes* has become so well established in the literature it is not proposed to

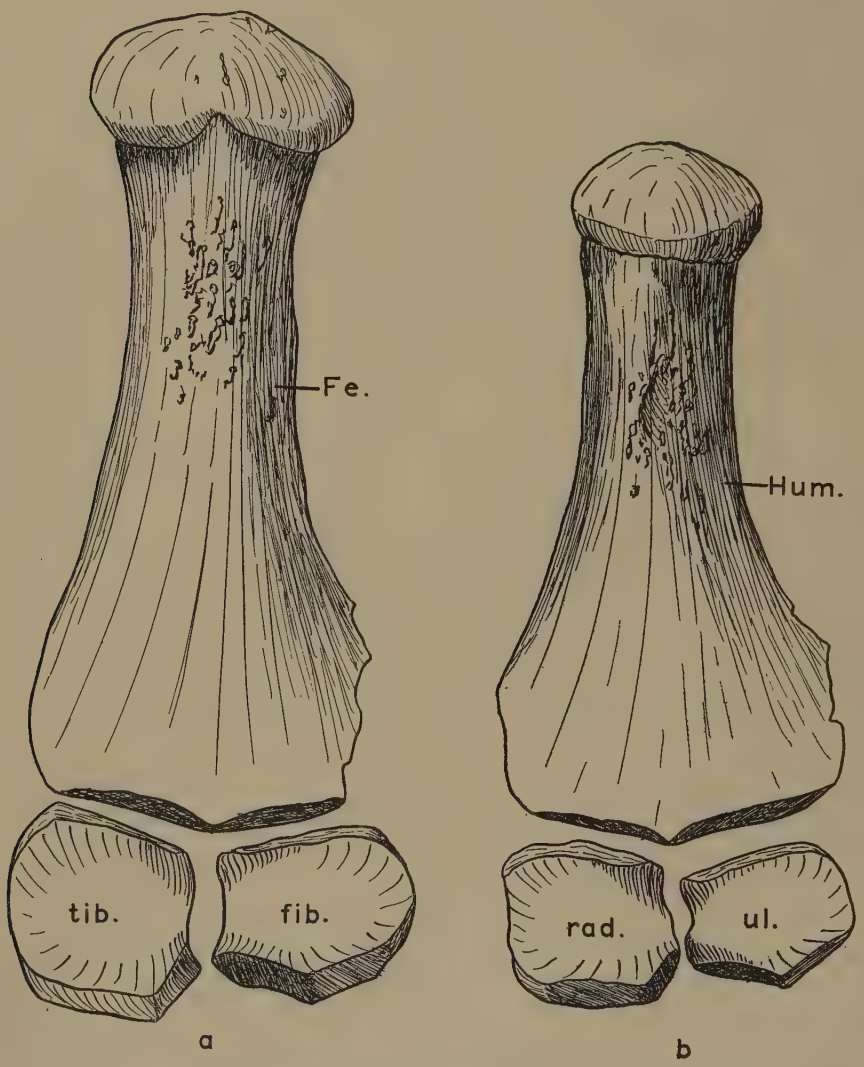


FIG. 9. *Peloneustes philarchus* (Seeley), holotype. J.46913, Sedgwick Mus. Propodials and epipodials in ventral view, × ¼. *a*. right hind limb ; *b*. right forelimb. HUM., humerus ; FE., femur ; fib., fibula ; rad., radius ; tib., tibia ; ul., ulna.

revise it. Jaccard (1908), Andrews (1913) and Linder (1913) described complete skeletons of *Peloneustes philarchus*, and Linder erected the new subspecies *Peloneustes philarchus* var. *spatyrhynchus* for a form in which the anterior part of the mandibular

symphysis was spatulate. The osteology of *Peloneustes philarchus* is known in detail, but the holotype itself has never been adequately described or figured. Since it is important to have a published record of the holotype, the skeleton originally listed by Seeley as *P. philarchus* is here figured and described for the first time.

DESCRIPTION OF HOLOTYPE. *Teeth.* A number of teeth are known from the type skeleton, but apart from one fragment (Pl. 26, fig. 3) all have the distal part of the crown missing. The fragment which is reasonably complete shows that most of the fine longitudinal ridges reach half-way up the crown, a few ridges only continuing to the tip. This character is extremely distinctive and serves to separate this species from the other known Oxfordian species. Andrews (1913 : 202) described such teeth in his description of material assigned to *Peloneustes philarchus*.

Mandible. The mandible measures 740 mm. in length. There are 38 alveoli preserved in the right ramus, but the immediate post-symphysial portion of the left ramus is missing. Thirteen to fourteen pairs of teeth are included in the symphysis of which the anterior 6–7 pairs are large and caniniform. This species has a comparatively longer mandibular symphysis than any other pliosaur and is generically separated from *Pliosaurus* on this account.

Cervical vertebrae. The articular surfaces of the cervical vertebrae are strongly concave with markedly bevelled margins. In several of the more anterior centra a pronounced ventral lip is developed, to which Lydekker (1889*b*) drew attention. In ventral view there is a distinct ventral keel in the mid-line. The cervical centra of *Pliosaurus evansi* are indistinguishable from these.

Pectoral girdle. The pectoral girdle is better known from specimens in the British Museum (Nat. Hist.) in which there is a triangular interclavicle in addition to the scapula and coracoids. Only the glenoid portions of the scapulae are preserved in the holotype, but I have figured a scapula here showing the typical form of the pliosaur scapulae with the dorsal process produced laterally and a ridge on the ventral surface extending towards the anterior part of the ventral plate.

Propodials and epipodials. All four limbs are preserved together with their epipodials and tarsal and carpal elements. A humerus and femur are figured together with their epipodials (Text-fig. 9). The epipodials are of considerable interest since the tibia and radius are greater in length than in width, whilst in the fibula and ulna the reverse is the case. Were these bones found isolated, the radii and tibiae would be considered Oxfordian in age, and the fibulae and ulnae Kimeridgian. Obviously there was considerable variation in this part of the skeleton since in other skeletons of this species all the epipodials are longer than they are broad.

Genus ***SIMOLESTES*** Andrews, 1909

EMENDED DIAGNOSIS. Mandible with very short spatulate symphysis bearing 5–6 pairs of large caniniform teeth ; total of approximately 25 teeth in each ramus. Scapula triradiate, dorsal process directed laterally. Epipodials long.

TYPE SPECIES : *Simolestes vorax* Andrews.

Simolestes vorax Andrews

(Pl. 27 ; Pl. 28, figs. 3–3*b*)

1909. *Simolestes vorax* Andrews, pp. 423–429, text-figs. 4–7.
1911. *Thaumatosaurus calloviensis* Bogolubov, pp. 200–203, pl. 2, figs. 1, 6.
1913. *Simolestes vorax* Andrews : Andrews, pp. 25–34, pl. 3, text-figs. 8–10.

EMENDED DIAGNOSIS. Teeth circular in section ; few longitudinal enamel ridges on outer surface (absent altogether in largest teeth), beginning part-way up the crown leaving a smooth area at the base of the outer surface. Cervical vertebrae short, length about half width or height, ventral keel absent.

MATERIAL. Holotype, R.3319, British Museum (Nat. Hist.), complete associated skeleton, Oxford Clay, Peterborough.

HISTORY OF THE SPECIES. Andrews (1909) erected this species and the new genus *Simolestes* on a complete skeleton of which he gave a careful description. Later (1913) he re-described and figured the type skeleton more fully. The original generic and specific descriptions have required no further revision. Discussion has tended to centre around the family position of the species. It was recognized by Andrews to be a fairly typical pliosaur. White (1940), however, placed it in the family Elasmosauridae—thus associating it with the most advanced forms of the long-necked plesiosaurians, but this is incorrect. Recently Romer (1956) also excluded *Simolestes* from the pliosaurs including it in a new family, the Thaumatosauridae based on the genus *Thaumatosaurus* which is shown below to be invalid. *Simolestes vorax* is certainly a pliosaur and an immature skeleton of the same species is described below, together with part of the holotype.

DESCRIPTION OF HOLOTYPE AND SKELETON OF IMMATURE INDIVIDUAL. *Teeth.* These are all circular in section and are ornamented by fine longitudinal ridges on the enamel : the ridges are more numerous on the inner surface of the crown and those on the outer surface always begin some distance from the base, so that there is a roughly semicircular area at the base of the outer surface of the crown which is devoid of ornament. This is a constant feature of the teeth of this species and can be used in its recognition. It should, however, be noted that in the very largest teeth there is often no ornamentation at all on the outer surface of the crown, and the teeth are then hardly distinguishable from those of *Pliosaurus andrewsi*.

Mandible. In the holotype, the snout of the animal is preserved with the mouth closed, so that it is not possible to see the mandible in dorsal view. The smaller individual (R.3170) has the mandible isolated and the symphysial portion is excellently preserved (Pl. 27, fig. 4). The symphysis is extremely short and so expanded that its 5 pairs of large caniniform teeth are set almost in a circle. I find it difficult to offer any functional explanation of this remarkable dentition.

Cervical vertebrae. The vertebral column of the holotype is preserved in natural articulation but the detailed characters of its cervical vertebrae have not previously been recorded. The cervical vertebrae of the immature specimen are so badly preserved as to be hardly recognizable. There is no ventral keel on the ventral surface ; on the anterior margin a ventral lip is produced anteriorly, but this only occurs in

the first few cervical centra. The articular surfaces are concave with a marginal bevel limited peripherally by a narrow groove. In lateral view, a faint ridge is developed extending from the apex of the triangular superior rib facet to the base of the neural arch.

Scapulae. The scapulae differ significantly from those of the other Oxfordian pliosaur species. The dorsal process is long and fairly narrow, directed posterolaterally, and set off from the plane of the rest of the bone. The ventral plate also forms a narrow process, about the same width as the dorsal process. It is not expanded to any degree and thus contrasts strongly with the scapula of *Peloneustes philarchus* and other Oxfordian pliosaurs.

Propodials. A humerus of the immature individual (Pl. 27, fig. 6) shows that the propodials differ from the holotype in that they do not possess the marked tuberosity midway down the posterior edge of their shafts. This feature was considered to be of diagnostic value by Tarlo (1958), but this view is erroneous. The propodials of *Simolestes vorax* are similar to those of most other pliosaurs and are valueless for the recognition of species.

Simolestes nowackianus Huene

1938. *Simolestes nowackianus* von Huene, pp. 370–376, text-figs. 1, 2.

EMENDED DIAGNOSIS. Teeth circular in section; ornamentation of fine closely packed longitudinal striations. Cervical vertebrae not known.

MATERIAL. Holotype, symphysial portion of mandible, Tubingen University Museum, Oxfordian, Abessinien.

HISTORY OF THE SPECIES. von Huene (1938) described a mandible similar to that of *S. vorax*. He suggested that the specimen represented a new species of *Simolestes* as the teeth were ornamented differently from those of *S. vorax*. Although no other parts of the skeleton are known von Huene's species *Simolestes nowackianus* may be accepted as a valid species.

III. SPECIES TEMPORARILY RETAINED

GAMMA. *Pleiosaurus gamma* Phillips

Type. Anterior cervical centrum from the Oxford Clay of Weymouth figured Phillips (1871, fig. 152).

Phillips (1871) erected this name to include a number of cervical, dorsal and caudal vertebrae from the Kimeridge Clay of Shotover and the Oxford Clay of Weymouth. Only the cervical vertebrae are sufficiently distinctive to be of any taxonomic value and the Weymouth centrum, J.10455 in the University Museum, Oxford, is here selected as the lectotype. The name *Pliosaurus gamma* Phillips is retained only for the two cervical centra from the Oxford Clay of Weymouth.

GROSSOUVREI. *Liopleurodon grossouvrei* Sauvage

Holotype. Tooth from Kellaways Rock, figured Sauvage (1873, pl. 7, fig. 2).

Lydekker (1889*b*) described several teeth from the Coral Rag of Heddington Wiltshire (one of which he figured) under the name *Pliosaurus grossouvrei* and commented that they were very probably identical with those of *Pliosaurus evansi* (= *P. andrewsi*). These teeth are assigned to *Pliosaurus andrewsi* and the name *L. grossouvrei* is retained for the holotype and all similar teeth from the Kellaways Rock.

IRGISENSIS. *Peloneustes irgisensis* Novozhilov

Holotype. Skull described and figured Novozhilov (1948 : 118, fig. 1*b*).

This species is based on a skull which differs from that of *Peloneustes philarchus* in several respects. These differences may well be due to the fact that Novozhilov was describing a skull of *Pliosaurus* under the impression gained from the literature, that only *Peloneustes* was long-snouted. Until further description of Novozhilov's specimen is forthcoming I prefer to place his species in the genus *Pliosaurus*. At the moment I am unable either to accept or reject the validity of his specific name.

ROSSICUS. *Pliosaurus rossicus* Novozhilov

Holotype. Skull described and figured Novozhilov (1948 : 115, fig. 1*a*).

Novozhilov described a pliosaur skeleton from the Lower Volgian to which he gave the new specific name *P. rossicus*. The main features of this specimen are that the teeth are trihedral in cross-section, thus confirming its Kimeridgian age ; the scapula, according to Novozhilov, is like that of *Kronosaurus* (i.e., like that of *Pliosaurus* L.B.T.), thus confirming the inclusion of the species in *Pliosaurus*. Only the skull is figured and there is no description of the mandibular symphysis. Furthermore there is no indication of the characters of the cervical vertebrae. Until more is known I hesitate to accept Novozhilov's species as valid.

IV. INVALID SPECIES

AEQUALIS. *Pleiosaurus aequalis* Phillips

Holotype. Femur from Kimeridge Clay of Swindon, figured Phillips (1871, fig. 164).

Lydekker (1889*b*) placed this species in the genus *Peloneustes*, thus extending the range of the genus into the Kimeridgian. Since I have found propodials to be of little taxonomic value, this species (based on an isolated limb bone) is here considered invalid, retaining *Peloneustes* as an Oxfordian form only. (*Peloneustes kanzleri* Koken is a Cretaceous Elasmosaur.)

ARCHIACI. *Polyptychodon archiaci* Deslongchamps

Type. Mandible from Kimeridge Clay of Le Havre, figured Deslongchamps (?1872, pl. 5, figs. 1, 2).

The same specimen was figured by P. Fischer (1869) under the name *Pliosaurus grandis* (Owen). The mandible figured by P. Fischer and by Deslongchamps has a short mandibular symphysis bearing 6 pairs of large caniniform teeth, and on this basis can be provisionally included in the Kimeridgian species *Stretosaurus macromerus* (Phillips).

CALLOVIENSIS. *Thaumatosaurus calloviensis* Bogolubov

Holotype. Tooth from the Callovian of Moscow, figured Bogolubov (1912, pl. 2, figs. 1, 6).

This tooth bears fine longitudinal enamel ridges which begin part-way up the crown on the external surface—a feature characteristic of *Simolestes vorax* Andrews. Consequently *T. calloviensis* is included in the synonymy of *S. vorax*.

EVANSI. *Pliosaurus evansi* Seeley

Holotype. Associated cervical vertebrae from the Oxford Clay of St. Neots, Cambridgeshire, described Seeley (1869).

Seeley (1877) described and figured part of the type skeleton noting the presence of a marked ventral keel on the centra. Lydekker (1890) referred the species to the genus *Peloneustes*, and later (1890*a*) recognized that the cervical vertebrae of *Peloneustes evansi* "can only be distinguished by their larger dimensions" from *P. philarchus* (Seeley).

Since the cervical vertebrae are the only parts of the skeleton by which the type specimens of *P. evansi* and *P. philarchus* can be compared, it appears that a single species is represented. In view of this, *P. evansi* is taken to be a subjective synonym of *Peloneustes philarchus*.

Lydekker (1890*a*) referred the large mandible figured by Phillips (1871) as *Pleiosaurus ?grandis*, to *Peloneustes evansi*. Andrews (1913) described under the name *Peloneustes evansi* an associated skeleton with a mandible similar to that figured by Phillips (1871). He noted that there were 11–12 pairs of teeth in the mandibular symphysis. In this feature, the mandible agrees closely with that of *Pliosaurus brachydeirus* Owen, the type species, and should therefore have been put in the genus *Pliosaurus*. The cervical vertebrae of the associated skeleton described by Andrews are dissimilar to those of Seeley's type of *Pliosaurus evansi*; they should therefore not have been given the name of *evansi*. The skeleton described by Andrews has consequently been made the holotype of a new species—*Pliosaurus andrewsi* (see p. 163).

FREARSI. *Spondylosaurus frearsi* Fischer de Waldheim

Holotype. Anterior cervical centrum from the Kimeridge Clay of the Moscow Basin, figured Fischer de Waldheim (1845, pls. 7, 8).

The material collected by Mr. Frears " an intelligent English gentleman resident in Moscow ", and described by Fischer de Waldheim, was at the same time identified by Owen (1845) as *Plesiosaurus brachyspondylus*. Lydekker (1889*b*), however, considered Fischer's species to be a synonym of the Oxfordian *Pliosaurus grossouvrei* (Sauvage). From a comparison of Fischer's original figures and the specimens of *Pliosaurus brachyspondylus* (Owen) described by Tarlo (1959), *Spondylosaurus frearsi* can be considered a synonym of Owen's species.

GIGANTEUS. *Plesiosaurus giganteus* Conybeare

The name *Plesiosaurus giganteus* was erected by Conybeare (1824*a*) to include all Plesiosaurians with shortened cervical vertebrae, and no types were designated and no descriptions given. The cervical vertebrae from the Kimeridge Clay of Weymouth, figured by Conybeare (1824) and the associated skeleton from the Kimeridge Clay of Market Rasen were included in this species, which has generally been considered invalid as it was insufficiently characterized.

GIGANTEUS. *Pliosaurus giganteus* Wagner

Holotype. Tooth described and figured Wagner (1852, pl. 20). This tooth has a pattern of longitudinal enamel ridges on its crown similar to *Liopleurodon ferox* Sauvage. The cross-section of the tooth is also circular, confirming its Oxfordian age. Lydekker (1889*b*) placed *P. giganteus* Wagner in the synonymy of the Kimeridgian *P. macromerus* Phillips, since the specific name had already been employed for pliosaur remains by Conybeare (1824*a*). Wagner's specimen differs from all Kimeridgian pliosaur teeth in having a circular cross-section to its crown and it is here considered conspecific with the Oxfordian species *Liopleurodon ferox* Sauvage.

GIGANTEUS. *Pliosaurus giganteus* Trautschold

Holotype. A tooth from the Oxfordian of the Moscow Basin, described and figured by Trautschold (1860, pl. 8, fig. 25).

This tooth is referred to *Liopleurodon ferox* Sauvage, Trautschold's trivial name being pre-occupied by Wagner (1852) and by Conybeare (1824*a*).

GRANDIS. *Plesiosaurus grandis* Owen

Syntypes. Three isolated propodials and a triradiate scapula, all of which can no longer be traced. Unfortunately none of this material was ever adequately described or figured. Owen (1841*a*) transferred the species to *Pliosaurus*, and later (1861, 1863) he considered *Pliosauris grandis* to be the type species. However, as Lydekker (1889*b*)

pointed out, there was no evidence that the types of *P. grandis* even belonged to pliosaurs. Clearly this species is invalid, being based on indeterminate material.

Unfortunately Owen (1869*a*) described and figured a large pliosaur mandible from the Kimeridge Clay under the name *Pliosaurus grandis*. This mandible has 6 pairs of large caniniform teeth in its symphysis, a character until now considered typical of *Pliosaurus*, although the type species *P. brachydeirus* has 10–12 pairs of teeth in the mandibular symphysis. Lydekker (1889*b*) placed the large mandible described by Owen in *Pliosaurus macromerus* Phillips to which species the mandible described by P. Fischer (1869) as *P. grandis* and by Deslongchamps (?1872) as *Polyptychodon archiaci*, is assigned.

The name *P. grandis* has most regrettably persisted and it is to be found in such recent works as White (1940), Welles (1943) and Piveteau (1955). It is an invalid specific name and material similar to that described by Owen in 1869 can be tentatively assigned to *Stretosaurus macromerus* (Phillips).

MERIANI. *Ischyrodon meriani* von Meyer

Holotype. Tooth from Oxfordian of Argau Canton, Switzerland, described and figured von Meyer (1856*a*, pl. 2, figs. 1–3).

The name was erected in 1838 by von Meyer but remained a *nomen nudum* until 1856. Meyer (1856*a*) considered the tooth to be of Bradfordian age but the associated invertebrate fossils suggest Oxfordian. Lydekker (1889*b*) provisionally referred Meyer's material to the Kimeridgian species *P. macromerus* on the basis of its size. The circular cross-section of the crown of *Ischyrodon meriani* indicates Oxfordian age rather than Kimeridgian, since all known Kimeridgian pliosaurs possess teeth with a characteristic trihedral section. The tooth figured by Meyer is here provisionally included in *Liopleurodon ferox* since it clearly does not belong to any of the other five well-known Oxfordian species.

MOSQUENSIS. *Thaumatosaurus mosquensis* Kiprijanoff

Type. Anterior cervical vertebra from Oxfordian of Moscow Basin figured Kiprijanoff (1883, pl. 14, fig. 1), here selected as lectotype.

Lydekker (1889*b*) included this species in the synonymy of *P. ferox*. If Kiprijanoff's figures are compared with the associated cervical vertebrae of *L. ferox* figured by Andrews (1913) it is evident that they are conspecific, thus *T. mosquensis* is here considered a subjective synonym of *L. ferox*.

NITIDUS. *Pleiosaurus nitidus* Phillips

Type. Posterior cervical centrum from Kimeridge Clay of Shotover, figured Phillips (1871, fig. 156).

Lydekker (1889*b*) considered this species to be an immature form, but he noted that it closely accorded with the posterior cervical centrum of *Pliosaurus brachyspondylus* (since erected as the neotype). Phillips' sketch seems to be very similar

to *P. brachyspondylus*, so I take *P. nitidus* to be a synonym of *Pliosaurus brachyspondylus* (Owen).

OOLITHICUS. *Thaumatosaurus oolithicus* Meyer

Syntypes. Miscellaneous fragments of teeth, jaws, ribs and vertebrae from the ? Oxfordian of Württemberg. These remains were described by von Meyer in 1841 but were not figured until 1856. The fragments figured are pliosaurian but are quite indeterminable, and both specific and generic names must be rejected.

Note on the Genus *Thaumatosaurus*.

The genus *Thaumatosaurus* was proposed by von Meyer (1841) to cover a collection of indeterminate pliosaur fragments from the lower part of the Upper Jurassic (or the top of the Middle Jurassic). Lydekker (1889*b*) accepted the validity of this genus and included within it a number of Plesiosaur species including the Liassic *Plesiosaurus cramptoni* Carte & Bailey, for which Seeley (1874) had earlier proposed the generic name *Rhomaleosaurus*. In 1910 Fraas described a complete skeleton of a Liassic plesiosaur under the name of *Thaumatosaurus victor*. This specimen is so beautifully preserved that it has found its way into most text-books of vertebrate palaeontology. Although *T. victor* is preserved in ventral view and *Rhomaleosaurus cramptoni* in dorsal, there is no doubt that they belong to the same genus. As Andrews (1922) recognized, *Rhomaleosaurus* is a valid generic name for plesiosaurians with long necks and comparatively large heads. *T. victor* Fraas should therefore be named *Rhomaleosaurus victor* (Fraas).

It is important for the genus *Thaumatosaurus* to be rejected as its continued use in the literature leads to a great deal of confusion.

PLANUS. *Pliosaurus planus* Hulke

Holotype. Scapula from Kimeridge Clay of Shotover, noted Hulke (1883), figured Lydekker (1889*b*, fig. 36).

This scapula (which Hulke associated with a coracoid from the Oxford Clay) belongs to an immature *Pliosaurus*. It is specifically indeterminate but for the sake of convenience is described here under *P. brachydeirus*. The specific name used by Hulke was preoccupied by Owen (1864) for a Cretaceous elasmosaur.

PORTLANDICUS. *Pliosaurus portlandicus* Owen

Type. Right hind limb from the Portland Oolite of the Isle of Portland, figured Owen (1869, pl. 4). This limb, as shown by Seeley (1871) does not belong to a pliosaur but to a plesiosaur. Lydekker (1889*b*) placed it in the genus *Cimoliosaurus*; Sauvage (1880) in *Muraenosaurus*; and Bogolubov (1912) in *Colymbosaurus*: Savage (1958) erroneously retains the species in the genus *Pliosaurus* but Delair (1959) following Bogolubov correctly referred it to the plesiosaur genus *Colymbosaurus*.

RECENTIOR. *Plesiosaurus recentior* Parkinson

In 1822, Conybeare read a paper to the Geological Society of London in which he recorded for the first time the presence of plesiosaurians with shortened neck vertebrae in the Kimeridge Clay. These remains were not given a name and the paper which contained figures of pliosaur vertebrae from Weymouth, was not published until 1824. In the meantime, Parkinson (1822) published a book and gave the name *Plesiosaurus recentior* to plesiosaurians with shortened cervical vertebrae. Subsequently the name *P. recentior* was attributed to Conybeare by von Meyer (1832) and to von Meyer by Lydekker (1889*b*). The objections to Conybeare's specific name *giganteus* (p. 176) are equally applicable to Parkinson's *P. recentior*; no specific name can be used to include all plesiosaurians with shortened neck vertebrae.

SIMPLEX. *Pleiosaurus simplex* Phillips

Holotype. Propodial from Kimeridge Clay of Shotover, figured Phillips (1871, fig. 165).

Although this bone belongs to a pliosaur, it is specifically indeterminate.

STERRODEIRUS. *Plesiosaurus sterrodeirus* Seeley

Holotype. A basi-occipital and six vertebrae, all reputedly associated, from the Kimeridge Clay of Ely, described Seeley (1869).

These remains were placed in the species *Peloneustes aequalis* (Phillips) by Lydekker (1889*b*). I would tentatively assign them to *Pliosaurus brachydeirus* on the presence of a well-marked ventral keel on the cervical centra.

SUPRAJURENSIS. *Polycotylus suprajurensis* Sauvage

Holotype. Propodial bone from the Upper Kimeridge Clay, figured Sauvage (1876, pl. 1).

This supposed humerus belonged to a pliosaur but it is impossible to determine its specific identity.

SUPRAJURENSIS. *Pliosaurus suprajurensis* Sauvage

Holotype. Anterior cervical centrum from the Portlandian of Boulogne-sur-Mer, figured Sauvage (1879, pl. 27, fig. 1). This centrum is characterized by a prominent ventral keel and it can be assigned to *Pliosaurus brachydeirus* on this feature. It is included in the synonymy of the type species. The trivial name *suprajurensis* had already been used by Sauvage in 1876.

TROCHANTERIUS. *Plesiosaurus trochanterius* Owen

Syntypes. Propodials from Kimeridge Clay of Wiltshire, described Owen (1839).

These limb bones were transferred to *Pliosaurus* by Owen (1841*a*). However, these propodials belong to a plesiosaur and not to a pliosaur, as was recognized by

Sauvage (1876) who included the species in *Cryptocleidus*, and Bogolubov (1912) in *Colymbosaurus*. Delair (1959) follows Bogolubov in placing the species in *Colymbosaurus*. It is worth noting here that Owen (1869) described a large crocodilian mandible under the name *Pliosaurus trochanterius*.

WEIYUANENSIS. *Sinopliosaurus weiyuanensis* Young

Holotype. Tooth described and figured Young (1942, pl. 1, figs. 17–19).

Young (1942) described and figured a pliosaur tooth under the name *Sinopliosaurus weiyuanensis* Young. From the figures the specimen appears to be indeterminable and therefore in my opinion both the generic and specific names erected by Young are invalid.

Subsequently Young (1946) described further plesiosaurian remains as belonging to the same species including a tooth which, from his description, may well belong to *Pliosaurus andrewsi*.

WOSINSKII. *Pliosaurus wosinskii* Fischer de Waldheim

Holotype. Teeth in fragment of jaw from the Kimeridgian of the Moscow Basin, figured Fischer (1846, pls. 3, 4).

The crowns of these teeth have the typical trihedral cross-section common to all pliosaurs of Kimeridge age. The remains come from the same locality as *Spondylosaurus frearsi* (= *P. brachyspondylus*) and they may well belong to the same species. I have therefore tentatively included them in the synonymy of *Pliosaurus brachyspondylus* (Owen).

V. KEY TO THE IDENTIFICATION OF PLIOSAURS

1. Family PLIOSAURIDAE: Distinguishable on shortness of cervical vertebrae, proportions of propodials and elongated ischia.

PLIOSAURIDAE

1a.

ELASMOSAURIDAE
(Upper Jurassic forms)

1b.

Cervical vertebrae in lateral view.

1c.
femur

1d.
humerus

1e.
femur

1f.
humerus

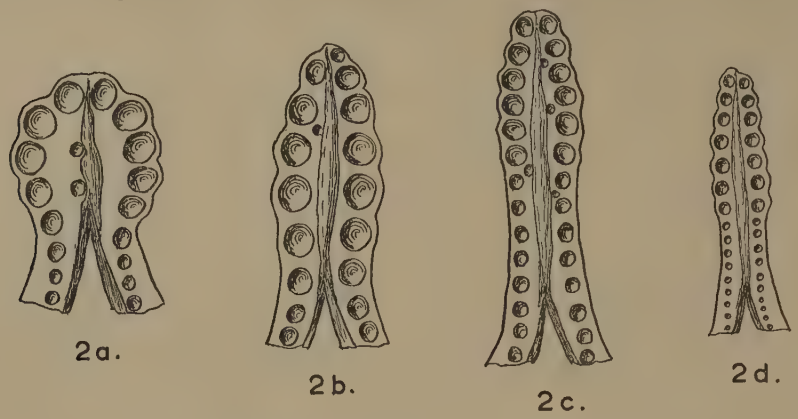
Propodials in dorsal view.

1g.

1h.

Ischia in dorsal view.

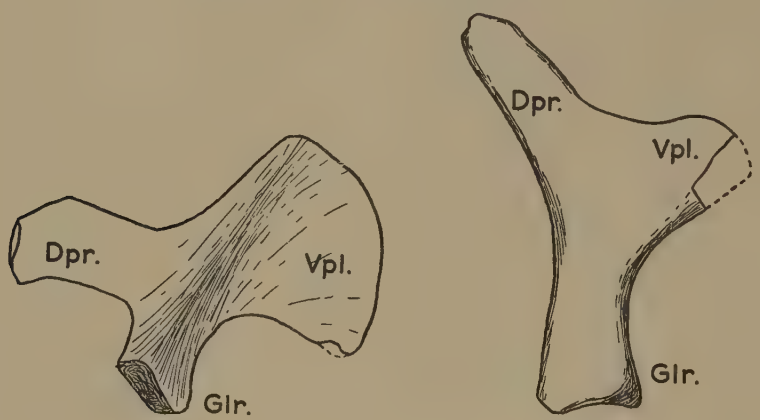
2. Genera : Pliosaur genera fall into four groups on the characters of the mandibular symphysis.



Simolestes *Liopleurodon-Stretosaurus* *Pliosaurus* *Peloneustes*

Mandibular symphyses in dorsal view.

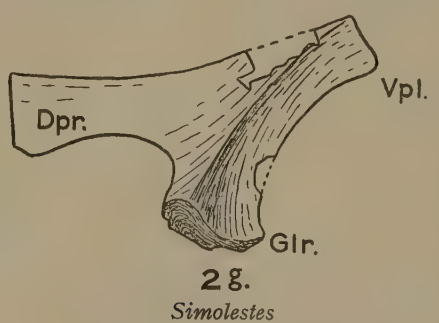
The genera *Liopleurodon* and *Stretosaurus* can be distinguished on their scapulae.



Scapulae in ventral view.

(Dpr., dorsal process ; Glr., glenoid ramus ; Vpl., ventral plate.)

All pliosaur genera (with the exception of *Stretosaurus*) have scapulae of *Liopleurodon* type, although this pattern may be slightly modified, as in *Simolestes*.



Scapula in ventral view.

3. Species: All pliosaurs can be separated into two groups on the cross-section of the crowns of their teeth. This is a horizontal division separating the Oxfordian species from those of Kimeridgian age.

3a.

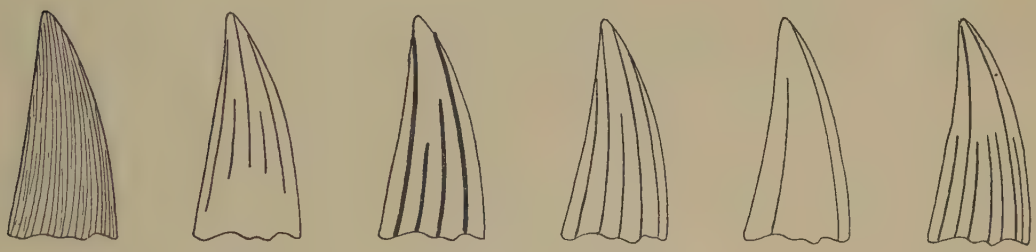
Oxfordian

3b.

Kimeridgian

Outline of teeth in cross-section.

The Kimeridgian species cannot be distinguished from one another by their teeth.
The Oxfordian species can readily be separated from one another on the ornamentation of the crowns of their teeth.



3c. *Simolestes nowackianus*

3d. *Simolestes vorax*

3e. *Liopleurodon ferox*

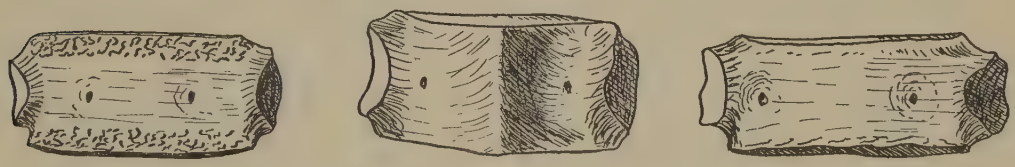
3f. *Liopleurodon pachydeirus*

3g. *Pliosaurus andrewsi*

3h. *Peloneustes philarchus*

Tooth crowns in external view.

The three Kimeridgian species can be separated on the character of their cervical vertebrae.



3j. *Pliosaurus brachyspondylus*

3k. *Pliosaurus brachydeirus*

3l. *Stretosaurus macromerus*

Cervical vertebrae in ventral view.

The specific distinctions of the Oxfordian pliosaurs can usually be supplemented by the characters of the cervical vertebrae.

3m.

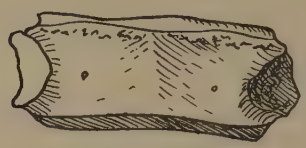
Peloneustes philarchus

3n.

Simolestes vorax-
Pliosaurus andrewsi

3p.

Liopleurodon ferox



3q.

Liopleurodon pachydeirus

Cervical vertebrae in ventral view.

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PLATE 20

Pliosaurus brachydeirus Owen, holotype, University Museum, Oxford.

FIG. 1. Mandible in dorsal view, J.9245B, $\times\frac{1}{7}$.

FIGS. 2–2*b*. Anterior cervical centrum, J.9294, $\times 1$; 2, anterior view, 2*a*, ventral view, 2*b*, lateral view of left side.

FIG. 3. Right femur in dorsal view, J. 9285, $\times\frac{1}{5}$.

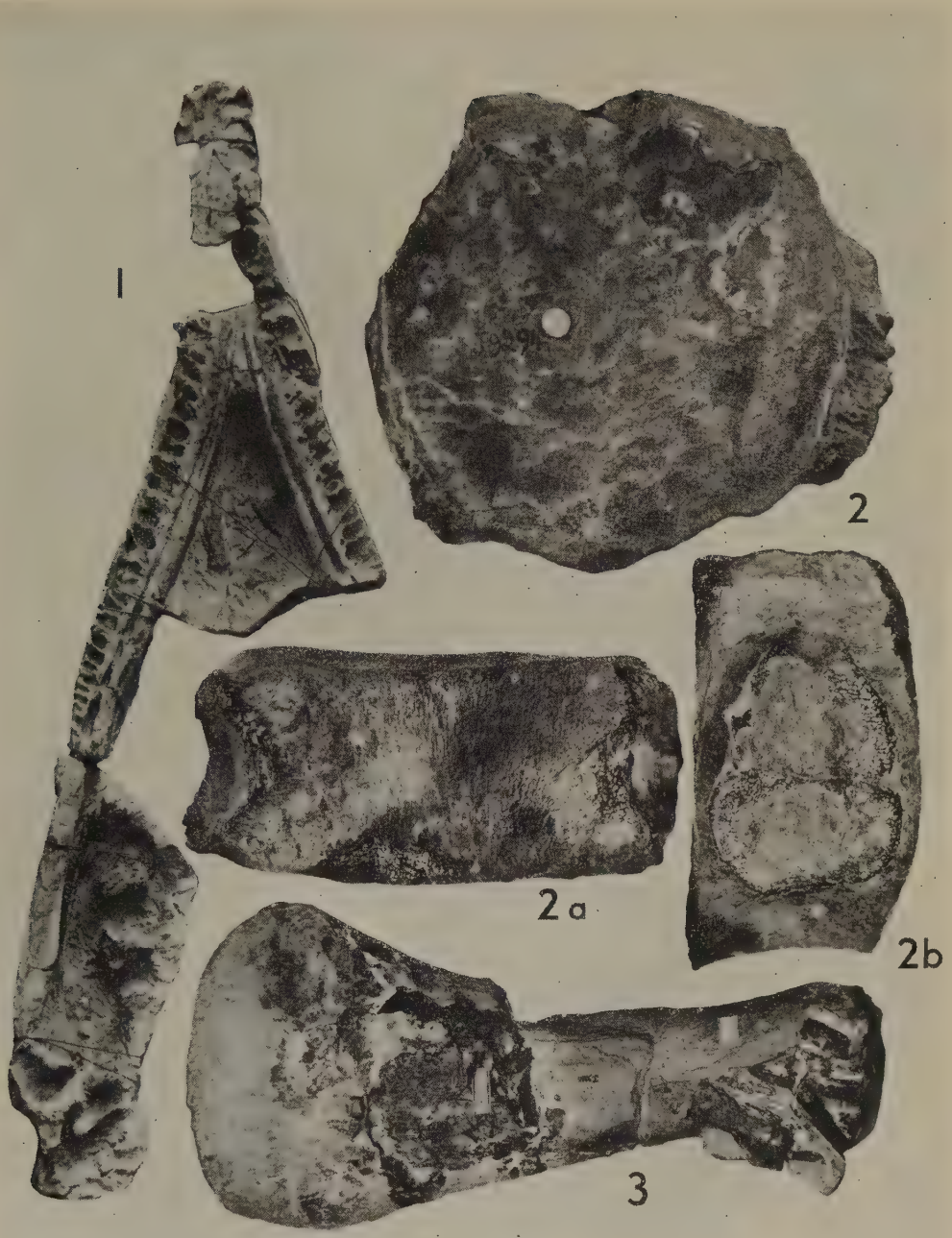
1
2
2a
2b
3

PLATE 21

Pliosaurus brachyspondylus (Owen), neotype, J.29564, Sedgwick Musuem, Cambridge.

FIGS. 1, 1*a*. Posterior cervical centrum, ×1; 1, anterior view, 1*a*, ventral view.
Associated skeleton, J. 35991, Sedgwick Museum, Cambridge.

FIG. 2. Mandible in dorsal view, × $\frac{1}{8}$.

FIGS. 3, 3*a*. Tooth ×1; 3 external view, 3*a*, lateral view.

FIG. 4. Left femur in dorsal view, × $\frac{1}{8}$.

Pliosaurus sp. FIG. 5. Right scapula R.287, Brit. Mus. (Nat. Hist.), in ventral view, × $\frac{1}{8}$.

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3
2
3a
1
1a
4
5

PLATE 22

Stretosaurus macromerus (Phillips), lectotype, J.10441, University Museum, Oxford.

FIGS. 1, 1*a*. Anterior cervical centrum, $\times\frac{1}{3}$. 1, anterior view, 1*a*, ventral view.

Associated skeleton, J.35990, Sedgwick Museum, Cambridge.

FIG. 2. Left scapula in ventral view, $\times\frac{1}{5}$.

FIG. 3. Anterior cervical centrum with cervical rib, in ventral view, $\times\frac{1}{3}$.

FIG. 4. Anterior cervical centrum, in posterior view, $\times\frac{1}{3}$.

Mandible J.10454, University Museum, Oxford.

FIG. 5. Dorsal view of symphysis, $\times\frac{1}{7}$.

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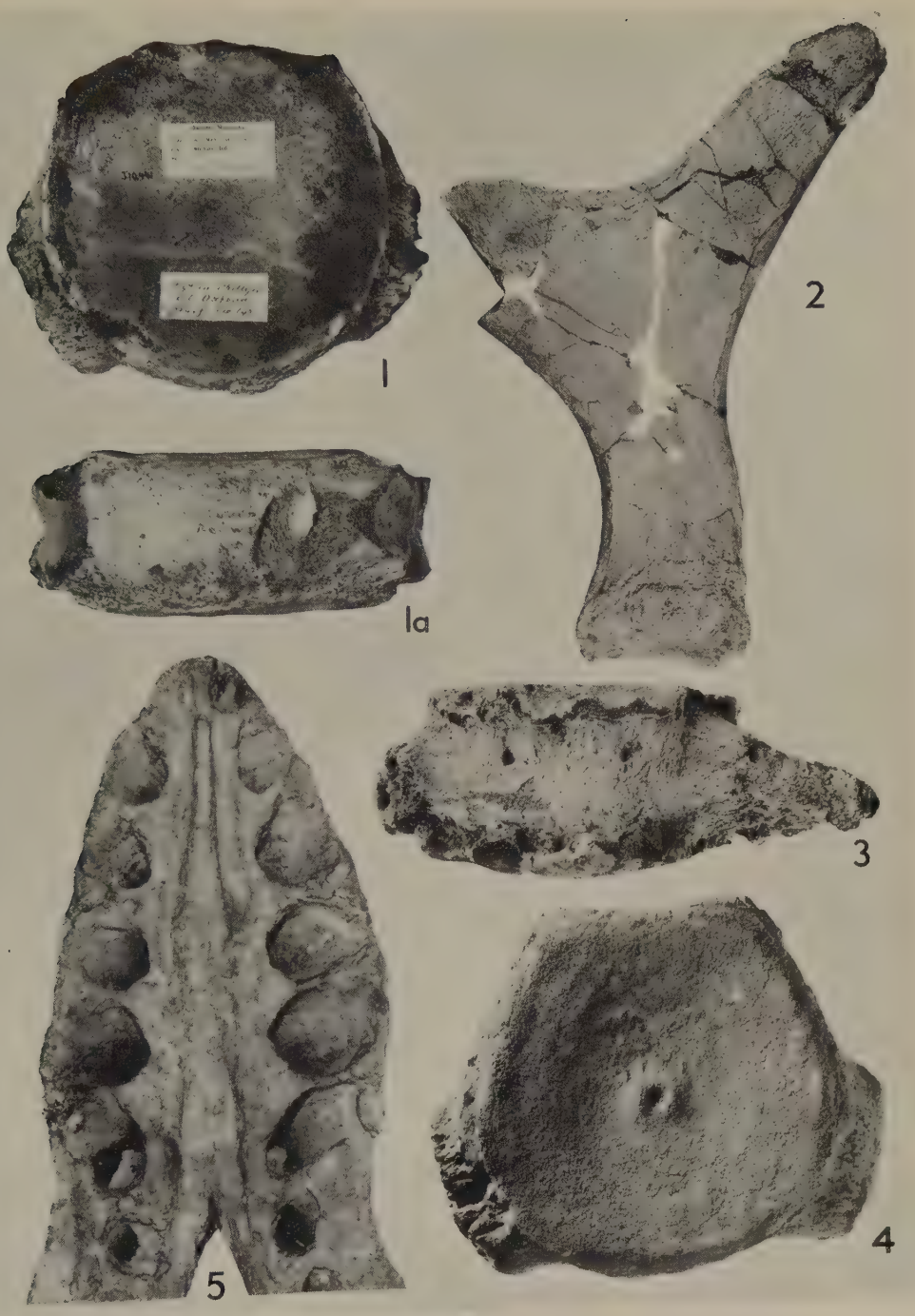
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1a
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PLATE 23

Pliosaurus andrewsi n. sp.

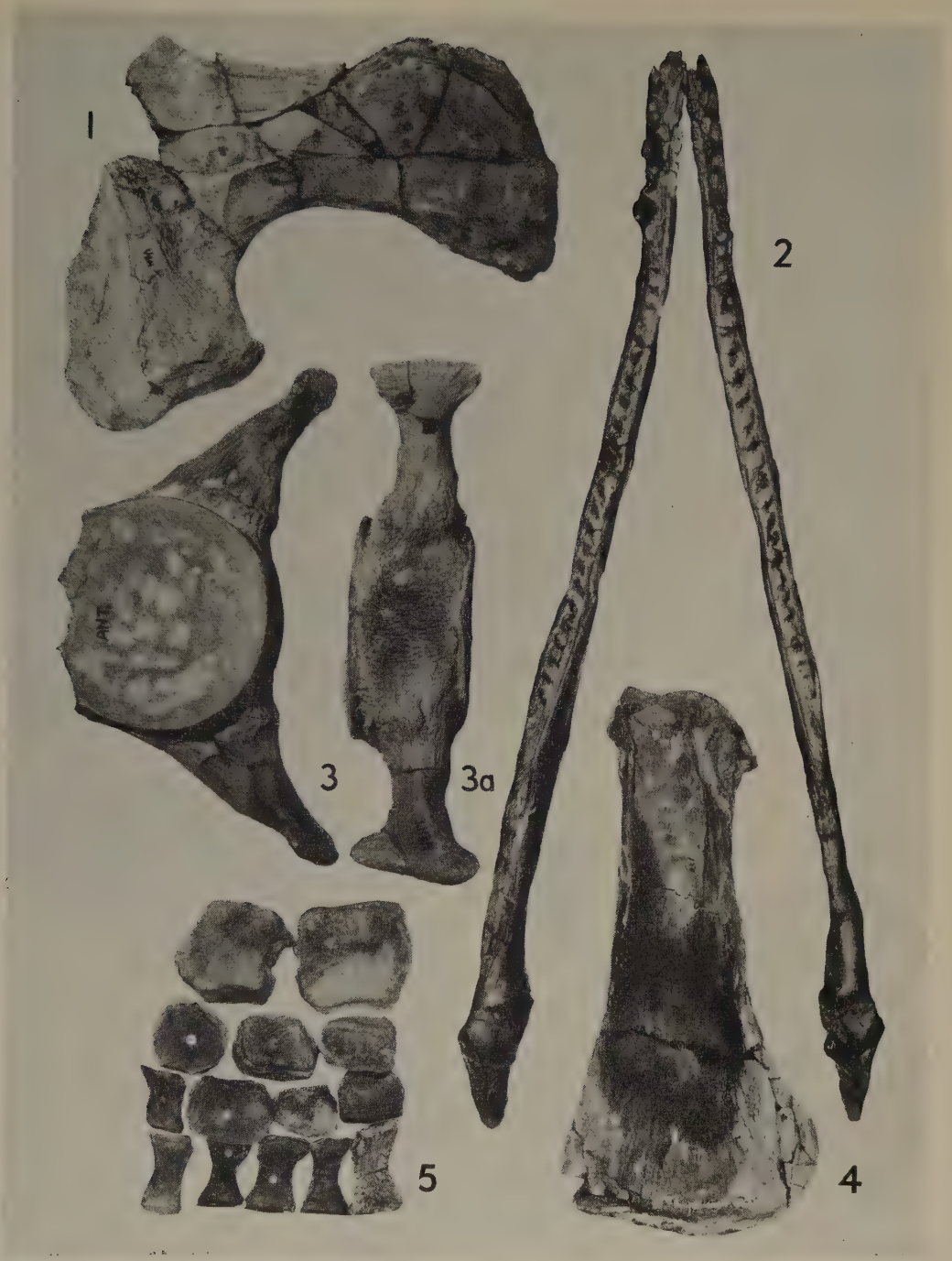
FIG. 1. Left scapula (R. 2437, Brit. Mus. (Nat. Hist.)) in ventral view, $\times\frac{1}{3}$. Holotype, R.3891, Brit. Mus. (Nat. Hist.).

FIG. 2. Mandible in dorsal view, $\times\frac{1}{6}$.

FIGS. 3, 3*a*. Anterior cervical centrum, $\times\frac{1}{2}$. 3, anterior view, 3*a*, ventral view.

FIG. 4. Left femur in dorsal view, $\times\frac{1}{6}$.

FIG. 5. Epipodials and tarsus of left hind limb in ventral view, $\times\frac{1}{6}$.


1
2
3
3a
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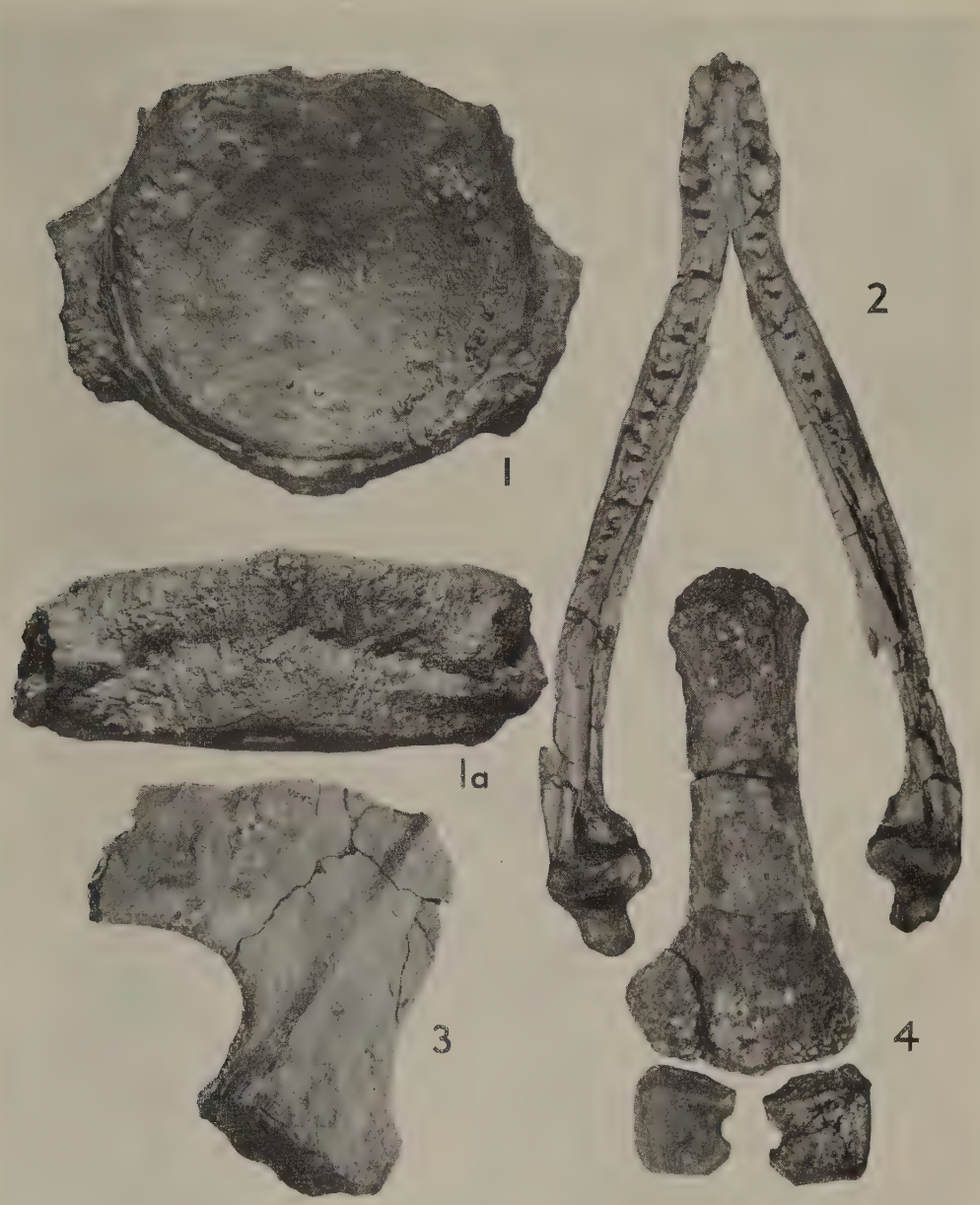
5

PLATE 24

Liopleurodon ferox Sauvage, associated skeleton, R.3536, Brit. Mus. (Nat. Hist.).

FIGS. 1, 1*a*, Anterior cervical centrum, $\times\frac{3}{4}$; 1, anterior view, 1*a*, ventral view.
FIG. 2. Mandible in dorsal view, $\times\frac{1}{10}$.
FIG. 3. Right scapula in ventral view, $\times\frac{1}{5}$.
FIG. 4. Right femur, tibia and fibula in dorsal view, $\times\frac{2}{9}$.


1
2
1a
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4

PLATE 25

Liopleurodon pachydeirus (Seeley), holotype, J.46912. Sedgwick Museum, Cambridge.

FIGS. 1, 1*a*, Anterior cervical centrum, $\times \frac{4}{5}$; 1, anterior view, 1*a*, ventral view.

Associated skeleton, R.2446, Brit. Mus. (Nat. Hist.).

FIGS. 2–2*b*. Anterior cervical centrum, $\times \frac{7}{8}$; 2, anterior view, 2*a*, ventral view, 2*b*, lateral view of left side.

FIG. 3. Mandible, dorsal view of symphysis, $\times \frac{1}{2}$.

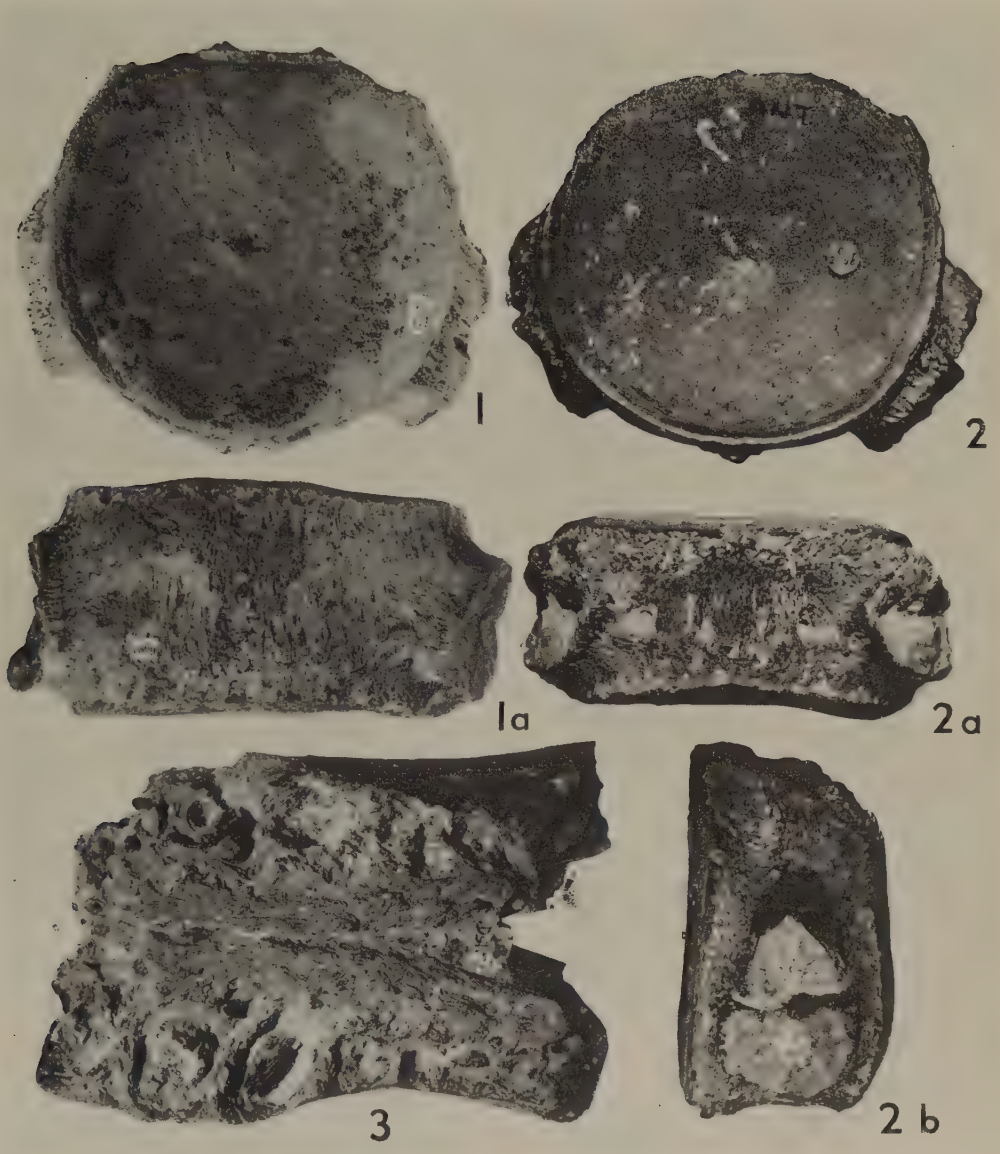
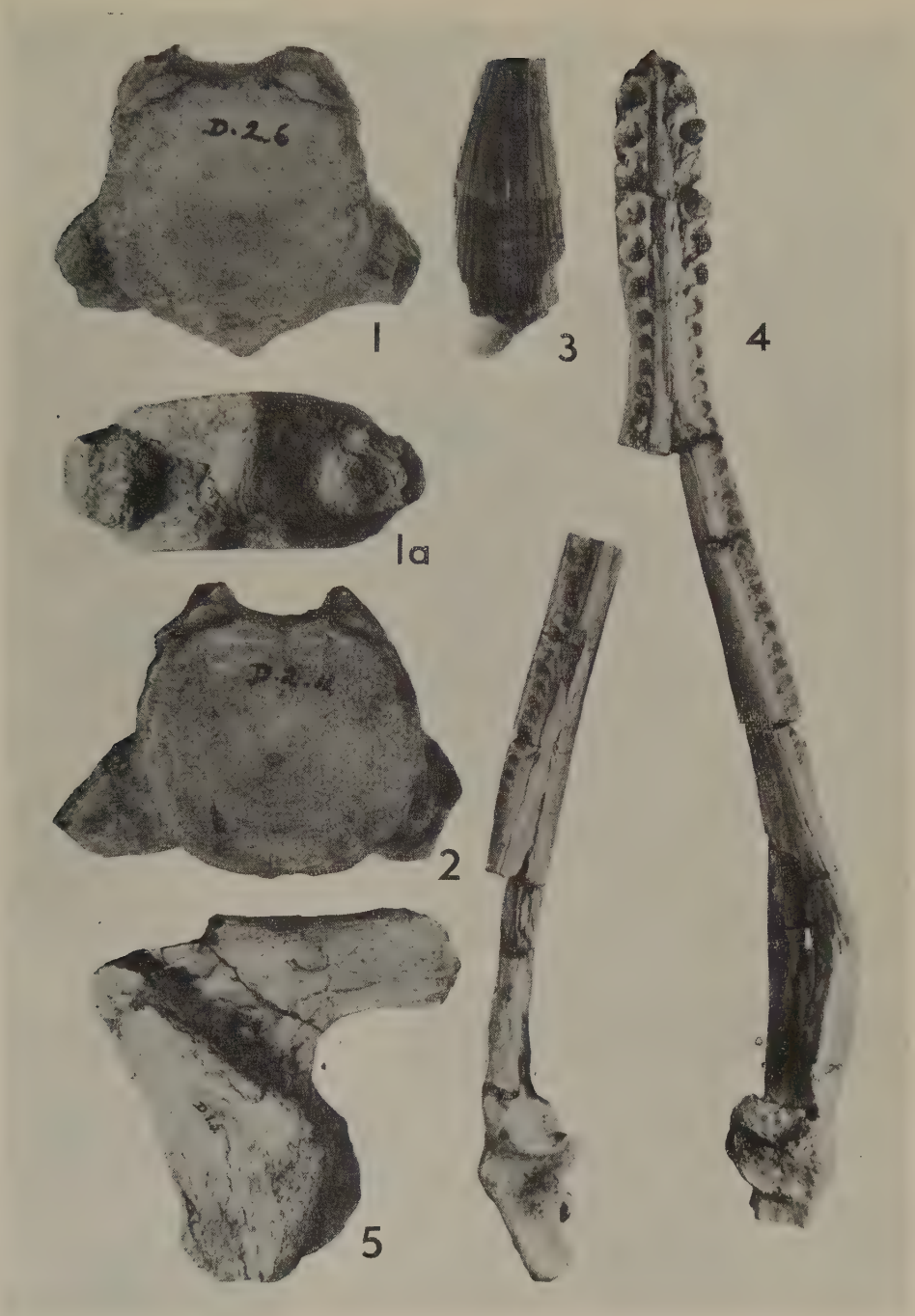

1
2
1a
2a
3
2 b

PLATE 26

Peloneustes philarchus (Seeley), holotype, J.46913, Sedgwick Museum, Cambridge.

FIGS. 1, 1*a*. Anterior cervical centrum, ×1 ; 1, anterior view, 1*a*, ventral view.
FIG. 2. Anterior cervical centrum, in anterior view, ×1.
FIG. 3. Fragment of crown of tooth, ×4.
FIG. 4. Mandible in dorsal view, ×$\frac{1}{2}$.
FIG. 5. Left scapula in ventral view, ×$\frac{1}{2}$.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1a
2
5

PLATE 27

Simolestes vorax Andrews, holotype, R.3319, Brit. Mus. (Nat. Hist.).

FIG. 1. Anterior cervical vertebra in lateral view, $\times \frac{1}{2}$.
FIG. 2. Anterior cervical vertebra in anterior view, $\times \frac{1}{2}$.
FIG. 3. Anterior cervical vertebrae in ventral view, $\times \frac{1}{3}$.
Associated skeleton, R.3170, Brit.Mus. (Nat. Hist.).
FIG. 4. Mandible in dorsal view, $\times \frac{1}{6}$.
FIG. 5. Left scapula in ventral view, $\times \frac{1}{3}$.
FIG. 6. Left humerus in dorsal view, $\times \frac{1}{3}$.

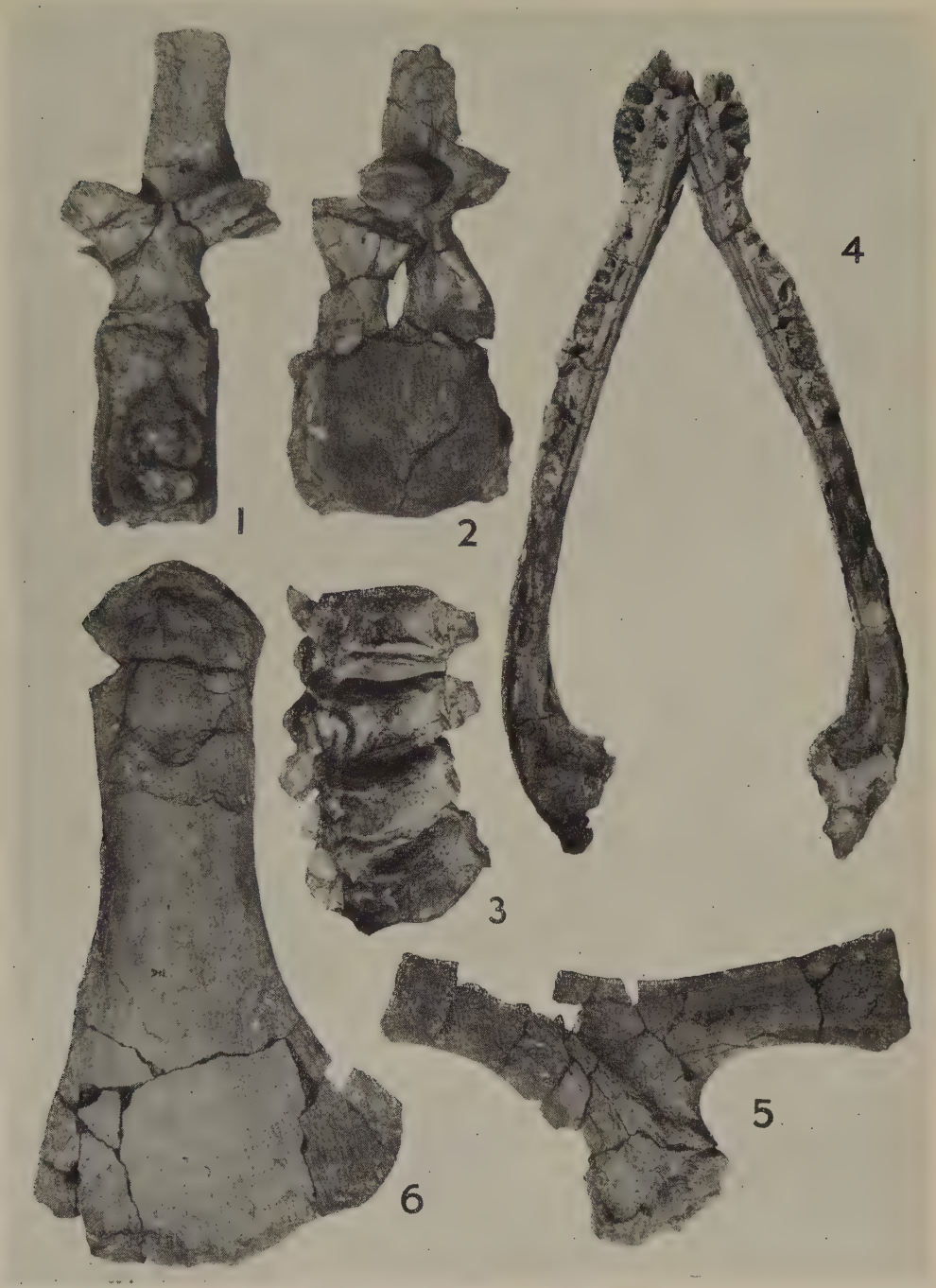
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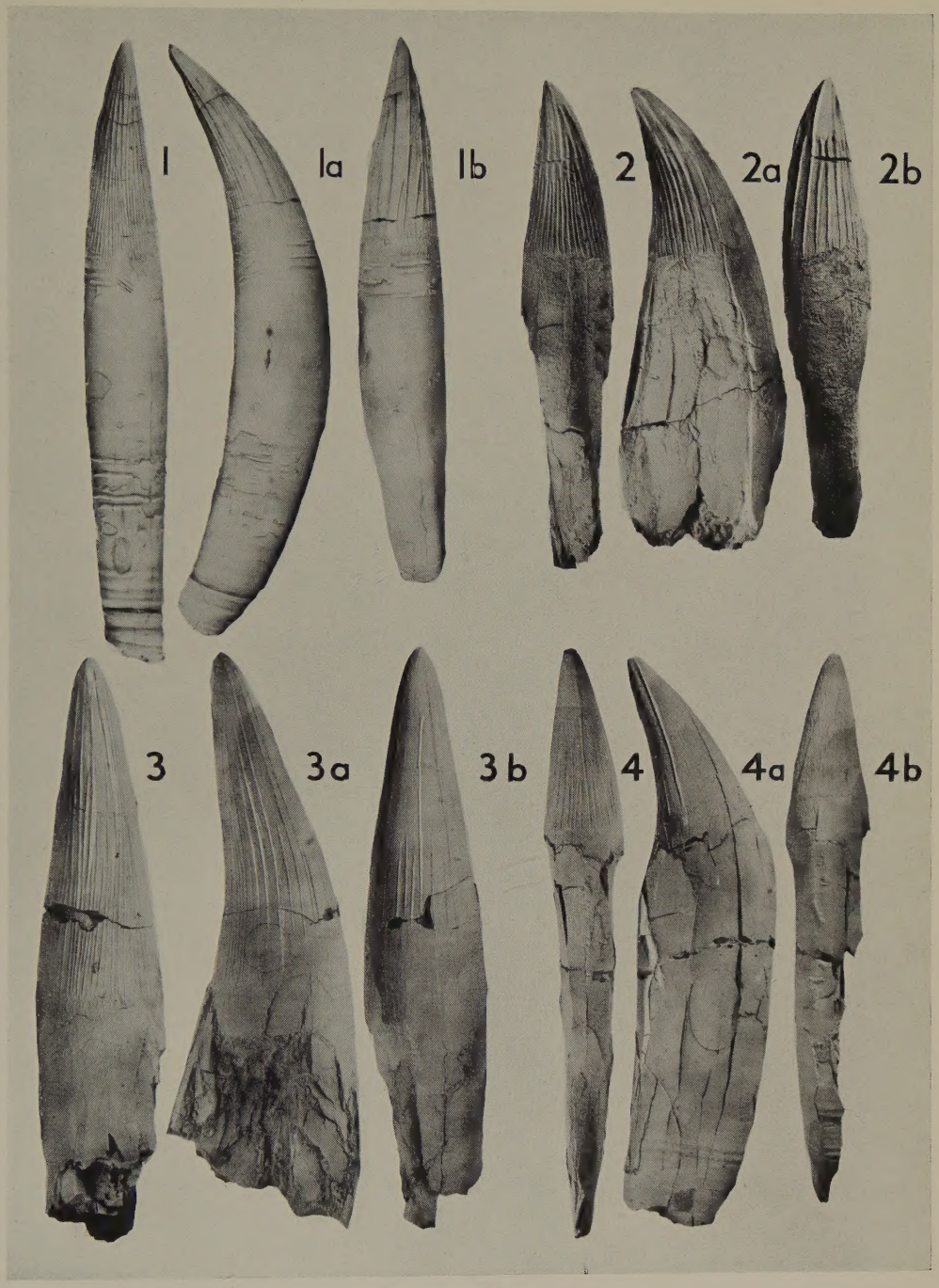
PLATE 28

FIGS. 1–1*b*. *Liopleurodon pachydeirus* (Seeley), tooth R.2446, Brit. Mus. (Nat. Hist.), $\times \frac{2}{3}$; 1, internal view, 1*a*, lateral view, 1*b*, external view.

FIGS. 2–2*b*. *Liopleurodon ferox* Sauvage, tooth R.3536, Brit. Mus. (Nat. Hist.), $\times \frac{2}{3}$; 2, internal view, 2*a*, lateral view, 2*b*, external view.

FIGS. 3–3*b*. *Simolestes vorax* Andrews, tooth, R.3170, Brit. Mus. (Nat. Hist.), $\times \frac{2}{3}$; 3, internal view, 3*a*, lateral view, 3*b*, external view.

FIGS. 4–4*b*. *Pliosaurus andrewsi*, n. sp., tooth, R.3891, Brit. Mus. (Nat. Hist.), $\times \frac{2}{3}$; 4, internal view, 4*a*, lateral view, 4*b*, external view.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